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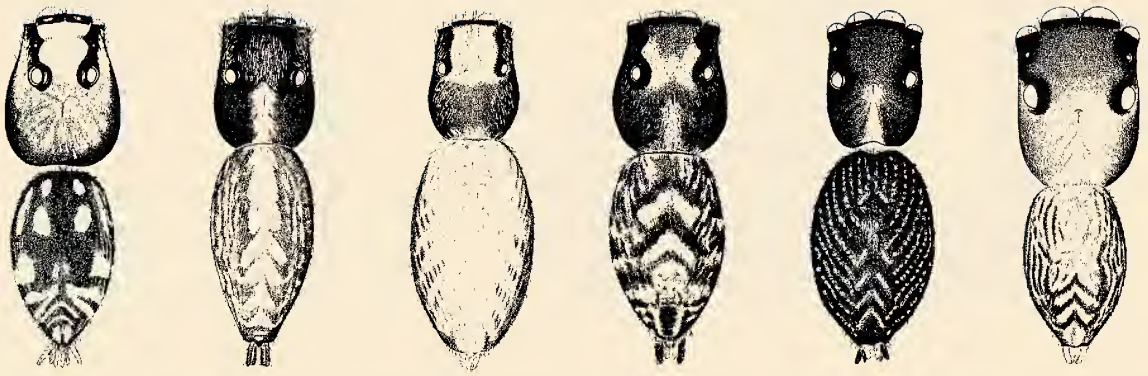

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Cover images—Comparison is an essential aspect of discovery in the natural sciences. In the example shown on the cover, Dr Marek Zabka has illustrated the cephalothorax and abdomen of six salticid spiders from southeastern Australia. Comparative studies involving these and many other Australian Museum specimens led him to conclude that five represent new species. They, and a number of others, were described by Dr Zabka in *Records of the Australian Museum* volume 54 (2002). The six images of body-form and pattern are, from left to right, *Arasia mullion, Helpis kenilworthi, H. risdonica, H. tasmanica, Sondra aurea*, and *S. samambrayi* (see full descriptions in Zabka, 2002, doi:10.3853/j.0067-1975.54.2002.1365).*

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Biogeographic and Biostratigraphic Implications of the *Serratognathus bilobatus* Fauna (Conodonta) from the Emanuel Formation (Early Ordovician) of the Canning Basin, Western Australia

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ABSTRACT. Discovery of *Serratognathus bilobatus* in the Early Ordovician Emanuel Formation of the Canning Basin, Western Australia, has regional biogeographic and biostratigraphic implications. Distribution of *Serratognathus* indicates a close biogeographic link between Australia and adjacent eastern Gondwanan plates and terranes during the latest Tremadocian to early Floian (Early Ordovician), and the formation of the so-called "Australasian Province", a distinctive biogeographic entity that existed throughout most of the Ordovician. The *S. bilobatus* fauna from the Canning Basin is much more diverse in comparison with those assemblages bearing *Serratognathus* from coeval Chinese Lower Ordovician successions and probably represents an assemblage inhabiting relatively deeper water (mid-outer shelf) environments. The Canning Basin fauna contains many pandemic forms, and bridges the gap in the regional correlation of this widely distributed fauna across eastern Gondwana.

This well-preserved, diverse fauna includes *Serratognathus bilobatus* and 23 associated species: *Acodus deltatus?, Acodus? transitans, Bergstroemognathus extensus, Cornuodus* sp., *Drepanodus arcuatus, Drepanoistodus* sp. cf. *D. nowlani, Fahraeusodus adentatus, Lissoepikodus nudus, Nasusgnathus dolonus, Paltodus* sp., *Paracordylodus gracilis, Paroistodus parallelus, Paroistodus proteus, Prioniodus adami, Protopanderodus gradatus, Protoprioniodus simplicissimus, Scolopodus houlianzhaiensis, Semiacontiodus* sp. cf. *S. cornuformis, Stiptognathus borealis, Triangulodus bifidus, Tropodus australis*, gen. et sp. indet. A and gen. et sp. B. A *P. adami-S. bilobatus* Biozone is defined within the middle and upper Emanuel Formation. Correlation of this biozone suggests an early Floian (late *P. proteus* Biozone to possibly earliest *P. elegans* Biozone) age for the middle and upper members of the Emanuel Formation.

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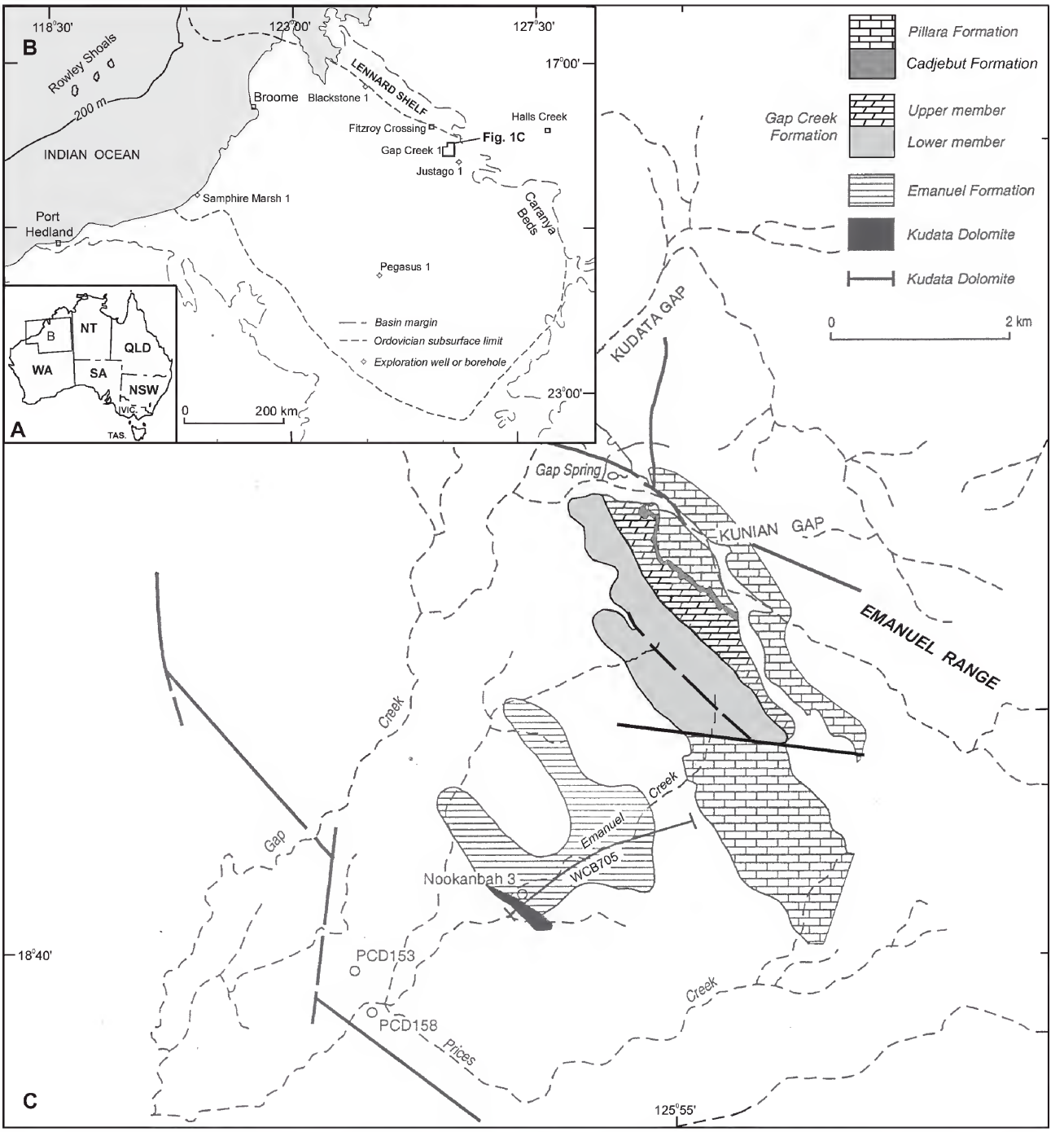

Fig. 1. Localities and geological maps of the studied area. (*A*), map of Australia showing location of the Canning Basin; (*B*), map of the Canning Basin; and (*C*), map of the Emanuel Creek area showing location of section WCB705 along Emanuel Creek (modified from Nicoll *et al.*, 1993).

Conodonts are abundant, diverse, and well-preserved in the Early Ordovician Emanuel Formation of the Canning Basin in Western Australia. In the nearly sixty years since the discovery of the fauna (Guppy & Öpik, 1950), this rich fauna has formed the subject of several important studies, particularly on the prioniodontids by McTavish (1973) and by Nicoll & Ethington (2004), rhipidognathids by Zhen *et al.* (2001), *Jumudontus brevis* by Nicoll (1992), and *Stiptognathus borealis* (Repetski, 1982) by Ethington *et al.* (2000). As documentation of the entire fauna represented by a huge collection recovered from several measured sections and subsurface core material is still in progress, the current contribution focuses only on *Serratognathus bilobatus* Lee, 1970 and the associated fauna recovered from three samples of the Emanuel Formation.

The discovery of *S. bilobatus* in the Emanuel Formation, which was deposited in relatively deep water, mid-outer shelf settings, provides crucial new biostratigraphic data to more precisely date and correlate the *Serratognathus* faunas widely distributed in eastern Gondwana and adjacent Peri-

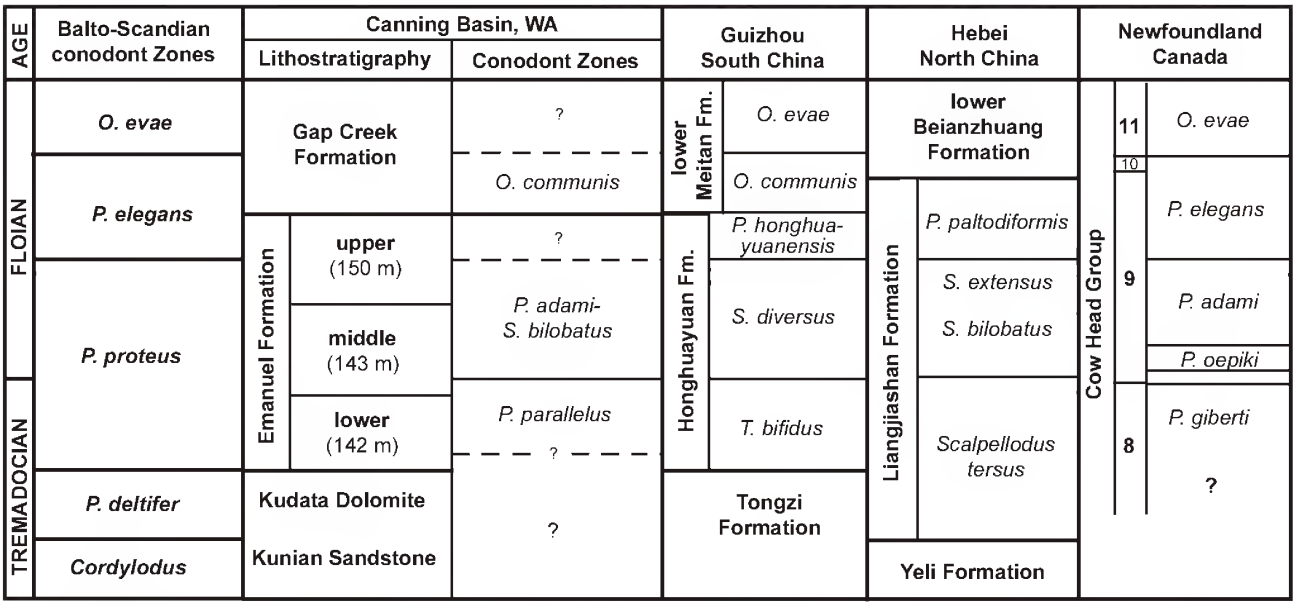

Fig. 2. Conodont biostratigraphy of the Emanuel Formation (late Tremadocian to early Floian, Early Ordovician) of the Canning Basin, and correlation with coeval successions in other regions in South China (Zhen *et al.*, in press a), North China (An *et al.*, 1983) and western Newfoundland (Stouge & Bagnoli, 1988).

Gondwanan plates and terranes. Regional correlation with coeval *Serratognathus*-bearing faunas from the Arafura Basin and from China, Korea and Malaysia, defines a distinctive Australasian Province in eastern Gondwana (Zhen *et al.* in Webby *et al.*, 2000) during the latest Tremadocian to early Floian (Early Ordovician). Moreover, as the *S. bilobatus* fauna from the Emanuel Formation contains a number of pandemic species, it serves as an ideal bridge correlating the *S. bilobatus* faunas in China and the more intensively studied Balto-Scandian and North American Mid-continent successions.

Regional geological setting and lithostratigraphy

The Canning Basin is an intracratonic sag basin, bounded by Precambrian rocks of the Kimberley Block to the north and the Pilbara Block to the south, occupying about one-sixth of Western Australia's onshore area (Fig. 1). Sparsely inhabited and covered largely by flat-topped hills and sand dunes, it is dominated by a Palaeozoic-Mesozoic sedimentary succession more than 15 km in thickness. Extensive geological investigations have been carried out in the region for more than a century (Purcell, 1984), spurred on by its high potential for fossil fuel reserves.

The Early Ordovician Prices Creek Group, representing the oldest stratigraphic unit in the basin, is only exposed along its northern margin (Lennard Shelf) where it rests unconformably on Precambrian basement. This basal contact is observable only in drillcore. The Prices Creek Group is overlain paraconformably by the Middle Devonian (Givetian) Cadjebut Formation (Hocking *et al.*, 1996). The group was initially subdivided into a lower Emanuel Limestone (subsequently renamed Emanuel Formation) and an upper Gap Creek Dolomite (later amended to Gap Creek Formation) with a measured thickness of 595 m for the Emanuel Formation in the type section along Emanuel Creek (Guppy & Öpik, 1950; Guppy *et al.*, 1958). Exploration drill holes in the area revealed an additional unexposed section between the Emanuel Formation and metamorphic rocks of the Precambrian basement, comprising a dolomitic interval 88 m thick underlain by 82 m of arkose (Veevers & Wells, 1961; Henderson, 1963; McTavish & Leg, 1976; Towner & Gibson, 1983). Nicoll *et al.* (1993) formally named the dolomitic unit the Kudata Dolomite and the arkose unit the Kunian Sandstone, and revised the Emanuel Formation as consisting of limestone intercalated with shale and siltstone with a total thickness of 435 m exposed in the type section (Fig. 1).

Regionally the Emanuel Formation conformably overlies the Kudata Dolomite and is conformably overlain by the Gap Creek Formation of mid-late Floian age (Fig. 2). The basal arkose of the Kunian Sandstone was deposited in a major transgressive phase flooding the Canning Basin during the Tremadocian (Nicoll *et al.*, 1993). This age determination was based on the regional tectonic framework and event stratigraphy, as well as fossil evidence from the overlying Kudata Dolomite, as no fossils were found in the arkose unit. The Emanuel Formation was subdivided into three informal members (Nicoll *et al.*, 1993). However, in the type area, both lower and upper members with intercalated shale, siltstone and limestone (or nodular limestone in the upper member) are poorly exposed, whereas the limestone-dominated middle member with a thickness of 143 m is better exposed forming a more or less continuous section. The Emanuel Formation has not only yielded a rich conodont fauna, but also trilobites (Legg, 1976; Laurie & Shergold, 1996a, 1996b), graptolites (Thomas, 1960; Legg, 1976), nautiloids (Teichert & Glenister, 1954), gastropods (Gilbert-Tomlinson, 1973; Jell *et al.*, 1984; Yu, 1993), brachiopods (Brock & Holmer, 2004) and various other invertebrate and microfossil groups (Guppy & Öpik, 1950; Brown, 1964; Schallreuter, 1993a, 1993b).

Table 1. Distribution of conodont species recovered from three samples in the Emanuel Formation of the Canning Basin, Western Australia.

species	WCB705/133	WCB705/243	161–166 m	Total
Acodus deltatus?	14	185	10	209
Acodus? transitans	4			4
Bergstroemognathus extensus	32	71		103
Cornuodus sp.	7	12	4	23
Drepanodus arcuatus	65	19	11	95
Drepanoistodus sp. cf. *D. nowlani*	30	13	9	52
gen. et sp. indet. A	10			10
gen. et sp. indet. B	1			1
Fahraeusodus adentatus	1		6	7
Lissoepikodus nudus	28	19	2	49
Nasusgnathus dolonus	19	6	5	30
Paracordylodus gracilis		35		35
Paltodus sp.	1			1
Paroistodus parallelus	180	256	21	457
Paroistodus proteus	16	12	2	30
Prioniodus adami	1	3		4
Protopanderodus gradatus	2	124		126
Protoprioniodus simplicissimus	8	17	3	28
Scolopodus houlianzhaiensis	3	5	11	19
Semiacontiodus sp. cf. *S. cornuformis*	18	4	4	26
Serratognathus bilobatus	5	1	1	7
Stiptognathus borealis	4	103		107
Triangulodus bifidus	1	2		3
Tropodus australis	77	83	30	190
total	527	970	119	1616

Age and correlation of the conodont fauna

McTavish (1973) described 20 multi-element conodont species and subspecies from the Emanuel Formation and lower part of the Gap Greek Formation; 19 of these were referred to prioniodontid genera, namely *Acodus, Baltoniodus, Prioniodus* and *Protoprioniodus*, and one to Periodontidae. On the basis of correlation with Balto-Scandian and North America Mid-continent successions McTavish (1973) determined a Latorpian age (latest Tremadocian to Floian in current terminology) for the Emanuel Formation and lower Gap Creek Formation. In particular, occurrence of *Acodus deltatus*?, *Paroistodus proteus* and *P. parallelus* in the Emanuel Formation allowed its correlation with the *Paroistodus proteus* Biozone (Hunneberg) of the Balto-Scandian succession, and the appearance of *Oepikodus communis* in the lower Gap Creek Formation supported correlation with the Ninemile Formation of central Nevada (McTavish, 1973, pp. 31, 32), namely the *O. communis* Biozone of the North America Mid-continent succession.

In our study 24 conodont species are documented from three samples in the middle and upper members of the Emanuel Formation (Table 1). *Paroistodus parallelus*, *Acodus deltatus*?, *Tropodus australis, Protopanderodus gradatus, Stiptognathus borealis, Bergstroemognathus extensus*, and *Drepanodus arcuatus* dominate the fauna, whereas *Serratognathus bilobatus* is relatively rare. As shown in Table 2, among the 24 species recorded in this study, 11 species were also recorded in the Honghuayuan Formation in the Yangtze Platform of South China (An, 1987, Ding *et al.* in Wang, 1993; Zhen *et al.*, in press a), seven in the Liangjiashan Formation of the North China Platform (An *et al.*, 1983), only three in the Qianzhongliangzi Formation of the Ordos Basin of North China Plate (An & Zheng, 1990), and four in the upper subgroup of the Qiulitag Group of the Tarim Basin (Zhao *et al.*, 2000). Recently a fauna closely comparable with that documented herein (with 12 species in common including *S. bilobatus*) was found in the Mooroongga Formation in the offshore Arafura Basin, north Australia (Nicoll unpublished material), indicating wide distribution of this species in western and northern Australia.

Jumudontus brevis Nicoll, 1992 ranges from the middle member to lower part of the upper member of the Emanuel Formation. It is a pandemic species, also found in Early Ordovician rocks in Utah and Texas (Ethington & Clark, 1982), Newfoundland (Stouge & Bagnoli, 1988), western Canada (Norford *et al.*, 2002), Baltoscandia (Bergström, 1988) and Greenland (Smith, 1991). In the Fillmore Formation of Utah, *J. brevis* first appears three m above the FAD of *O. communis* and extends to 237.7 m above the base of the formation at section H, suggesting a correlation with the lower *O. communis* Biozone (Ethington & Clark, 1982). In Newfoundland, it occurs in the upper part of Bed 9 (upper *P. elegans* Biozone) and lower part of Bed 11 (*O. evae* Biozone) of the Cow Head Group (Stouge & Bagnoli, 1988), an interval slightly higher than its occurrence (= upper *P. proteus* Biozone to lower *P. elegans* Biozone) in the Emanuel Formation.

Stiptognathus borealis (Repetski, 1982) is present from the upper part of the middle member to the basal part of the upper member of the Emanuel Formation, a range slightly shorter than that of *J. brevis* (Ethington *et al.*, 2000; Nicoll & Ethington, 2004). It was also recorded from the Great Basin (Ethington & Clark, 1982; Ethington *et al.*, 2000), western

Table 2. Comparison of occurrence of conodont species of the *Serratognathus* fauna from the Emanuel Formation with their distribution in other *Serratognathus* faunas recognized in China and other coeval successions referred to in the text.

species	mid-upper part of Emanuel Formation	Mooroongga Formation Arafura Basin	*S. diversus* Zone South China	*S. bilobatus* Zone North China	mid Qian-zhongliangzi Formation Ordos Basin	Qiulitag Group Tarim Basin	upper Dakui Formation Hainan	Setul Limestone Malaysia	*P. adami* Zone Bed 9 Newfoundland
Acodus deltatus?	•	•							
Acodus? transitans	•								
Bergstroemognathus extensus	•	•	•	•	•	•			•
Cornuodus sp.	•								
Drepanodus arcuatus	•	•	•	•					•
Drepanoistodus sp. cf. *D. nowlani*	•		•						
gen. et sp. indet. A	•								
gen. et sp. indet. B	•								
Fahraeusodus adentatus	•								
Lissoepikodus nudus	•	•							
Nasusgnathus dolonus	•	•	•	•		•			
Paracordylodus gracilis	•								•
Paltodus sp.	•								
Paroistodus parallelus	•						•		•
Paroistodus proteus	•	•	•	•					•
Prioniodus adami	•	•?							•
Protopanderodus gradatus	•	•	•	•					•
Protoprioniodus simplicissimus	•	•	•						•
Scolopodus houlianzhaiensis	•	•	•	•	•		•		
Semiacontiodus sp. cf. *S. cornuformis*	•		•						
Serratognathus bilobatus	•	•	•	•	•	•	•	•	
Stiptognathus borealis	•								
Triangulodus bifidus	•	•	•			•			
Tropodus australis	•								•

Texas (Repetski, 1982), and the Argentine Precordillera (Lehnert, 1995; Albanesi in Albanesi *et al.*, 1998). According to Ethington *et al.* (2000), it occurs in the Fillmore Formation of Utah, in the upper quarter of the El Paso Group and in the upper member of the Marathon Limestone of Texas, and in the Mountain Springs Formation of Nevada, constrained within an interval of upper *Acodus deltatus/Oneotodus costatus* Biozone to lower *O. communis* Biozone (early Floian age). However, in the Argentine Precordillera, earliest occurrence of *S. borealis* occurs in the upper *P. proteus* Biozone within the Tremadocian/Floian boundary interval.

Scolopodus houlianzhaiensis An & Xu in An *et al.*, 1983 occurs abundantly in the Liangjiashan Formation of North China with a similar stratigraphic range to that of *Serratognathus bilobatus* (An *et al.*, 1983), and was also reported from the Honghuayuan Formation in Guizhou (South China) in association with *Serratognathus diversus* (Zhen *et al.*, in press a). As both the Liangjiashan Formation and Honghuayuan Formation were deposited in shallow subtidal settings, faunas recovered from these two units are dominated by endemic forms, and it is difficult to directly correlate them with either the Balto-Scandian or North American Mid-continent successions. Thus the presence of *S. houlianzhaiensis* in association with *Serratognathus bilobatus* in the Emanuel Formation is critical to bridging this correlation gap.

Triangulodus bifidus Zhen in Zhen *et al.*, 2006 is a morphologically distinctive species occurring throughout the Honghuayuan Formation and also into the lower part of the overlying Meitan Formation in South China (Zhen *et al.*, 2006, 2007a). It is apparently a rare species in the Emanuel Formation, represented by only a few specimens (Fig. 15I–K), and will be reported from the *S. bilobatus* fauna in the Arafura Basin of northern Australia (Nicoll unpublished material).

Co-occurrence of *Paroistodus proteus* and *P. parallelus* in the Emanuel Formation also suggests a correlation with the upper part of the *P. proteus* Biozone of the Balto-Scandian succession. Löfgren (1997) indicated that in Sweden, *Paroistodus parallelus* makes its first appearance in the uppermost *P. proteus* Biozone, often associated with *P. proteus*, and extends to the upper middle *O. evae* Biozone. More specifically, occurrence of *Prioniodus adami* in the upper part of the Emanuel Formation allows a direct correlation with the *P. adami* Biozone (= upper *P. proteus* Biozone) recognized in the Cow Head Group of Newfoundland (Stouge & Bagnoli, 1988). There, *P. adami* was reported ranging through the lower to upper part (but not top) of Bed 9 in the Ledge-Point of Head Section (Stouge & Bagnoli, 1988, fig. 3), and the *P. adami* Biozone (succeeded by the *P.*

elegans Biozone) is characterized by abundant *P. adami* in association with *Bergstroemognathus extensus*, *Drepanodus arcuatus*, *Paroistodus parallelus*, *P. proteus*, *Paracordylodus gracilis*, *Tropodus australis*, *Protopanderodus gradatus*, and *Protoprioniodus simplicissimus*, all of which are also present in the Emanuel Formation. According to Stouge & Bagnoli (1988, figs 3,4), both *O. communis* and *P. elegans* first appear at a similar level in the upper part (not top) of Bed 9 and define the boundary of the *P. adami*/*P. elegans* biozones in the upper part of Bed 9. Both *P. proteus* and *P. parallelus* make their first appearance near the base of Bed 9 of the Cow Head Group, about three m below the first appearance of *P. adami*.

The first appearance (FAD) of *Tetragraptus approximatus* is the primary marker defining the base of the Floian Stage (Bergström *et al.*, 2004). In the Diabasbrottet GSSP Section at Hunneberg, southwestern Sweden, the Tremadocian/Floian boundary was defined by the FAD of *T. approximatus*, 2.1 m above the top of the Cambrian, and the lower part of the *T. approximatus* graptolite Biozone was correlated to the topmost subzone (*Oelandodus alongatus-Acodus deltatus deltatus* Subzone) of the *P. proteus* conodont Biozone (see Bergström *et al.*, 2004, fig. 10). Therefore, the FAD of *T. approximatus* near the base (3m above the base at the Ledge Section) of Bed 9 in the Cow Head Group (Williams *et al.*, 1999) suggests that the *P. adami* Biozone in Newfoundland should be correlated with the upper part of the *P. proteus* Biozone (*Oelandodus alongatus-Acodus deltatus deltatus* Subzone) of the Balto-Scandian succession.

The *P. adami-S. bilobatus* Biozone is proposed herein to represent the fauna from the middle to upper part of the Emanuel Formation. It is characterized by the occurrence of *P. adami*, *S. bilobatus, Paroistodus proteus, P. parallelus* and other species listed in Table 1, with its base defined by the first appearance of *S. bilobatus* from the middle member of the Emanuel Formation and the upper boundary defined by the first appearance of *O. communis* in the basal part of the Gap Creek Formation (Nicoll & Ethington, 2004). It can be confidently correlated with the *P. adami* Biozone in the lower part of Bed 9 of the Cow Head Group in Newfoundland, with the *Oelandodus alongatus-Acodus deltatus deltatus* Subzone of the *P. proteus* Biozone (possibly also lowest *P. elegans* Biozone) of the Balto-Scandian conodont succession, with the *S. diversus* Biozone in the Honghuayuan Formation of South China, and with the *S. bilobatus* and *S. extensus* biozones in the Liangjiashan Formation of North China (Fig. 2).

Biogeographic distribution of *Serratognathus*

The morphologically distinctive conodont *Serratognathus* is widely distributed in Lower Ordovician (lower Floian) rocks in China (South China, North China Platform, Ordos Basin, Tarim Basin and southern Hainan Island), Korea, Malaysia, and Australia (Arafura Basin and Canning Basin). Among the three species assigned to the genus (*S. bilobatus* Lee, 1970, *S. diversus* An, 1981, and *S. extensus* Yang in An *et al.*, 1983), *S. bilobatus* has a relatively wider geographic distribution (Fig. 3) occurring in the Dumugol Formation of South Korea (Lee, 1970), in the Liangjiashan Formation of North China Platform (An *et al.*, 1983), in the Qianzhongliangzi Formation of the Ordos Basin in North China (An & Zheng, 1990), in the Honghuayuan Formation of South China (An *et al.*, 1983; Ding *et al.* in Wang, 1993), in the upper part of the Dakui Formation of Sanya, Hainan Island (Wang *et al.*, 1996), in the lower part of the Setul Limestone in Malaysia (Metcalfe, 1980, 2004), in the Mooroongga Formation (subsurface) of the Arafura Basin off the north coast of Australia (Nicoll unpublished material), and in the Emanuel Formation of the Canning Basin, Western Australia (this study). Zhylkaidarov (1998, p. 65) indicated the occurrence of *S. bilobatus* from the Shabakty Formation in Malyi Karatau of southern Kazakhstan. However, as neither illustrations nor other information of the species from this locality are available, this Kazakhstan occurrence is considered doubtful at present. *Serratognathus diversus* is recorded in the Honghuayuan Formation and coeval units in South China (An *et al.*, 1985; An, 1987; Zhen *et al.*, in press a), Liangjiashan Formation of North China (An *et al.*, 1983), and the upper subgroup of the Qiulitag Group of the Tarim Basin (Zhao *et al.*, 2000). *Serratognathus extensus*, possibly representing the most advanced of the three species, has been reported only from the Liangjiashan Formation of North China Platform (An *et al.*, 1983).

The type material of *S. bilobatus* was described from the Dumugol Formation in the Taebaeksan Basin in the central-eastern part of the Korean Peninsula (Lee, 1970; Choi *et al.*, 2005). The Dumugol Formation (also called the Dumugol Shale) consists of shale and intercalated limestone whose thickness varies from 150 to 270 m across the region and contains cyclic successions shifting from the near-shore to the deeper subtidal facies on a low-relief carbonate shelf, which was believed to be part of an extension of the North China Platform during the Early Ordovician (Choi *et al.*, 2001, 2005). It yielded abundant conodont and trilobite faunas closely comparable to the late Tremadocian to early Floian faunas of North China (Lee, 1970, 1975; An *et al.*, 1983; Zhou & Fortey, 1986; Seo *et al.*, 1994; Choi *et al.*, 2005). Occurrence of the *Archaeoscyphia-Calathium* association (occasionally forming isolated bioherms) in the Dumugol Formation also supports a close biogeographic link with North China (Choi *et al.*, 2005). Based on rich and diverse conodont assemblages, Seo *et al.* (1994) divided the Dumugol Formation into four conodont biozones (in ascending order): *Chosonodina herfurthi-Rossodus manitouensis* Biozone, *Colaptoconus quadraplicatus* Biozone, *Paracordylodus gracilis* Biozone, and *Triangulodus dumugolensis* Biozone, with an age ranging from late Tremadocian to early Floian. They correlated the *Triangulodus dumugolensis* Biozone at the top of the Formation to the *S. bilobatus* Biozone of North China, but unfortunately *S. bilobatus* was not recovered from any of their studied samples, and the type horizon of this species described by Lee (1970) in the region was not pinned down in their new biostratigraphic scheme of the Dumugol Formation. However, Seo *et al.* (1994, p. 606) indicated that *S. bilobatus* also occurs in the overlying Maggol Formation as reported in two unpublished postgraduate theses.

In North China, *S. bilobatus* was widely reported as occurring in the Liangjiashan Formation within an interval correlated to the upper *P. proteus* Biozone to lower *P. elegans* Biozone of the Balto-Scandian conodont succession (Zhen *et al.*, in press a). The Liangjiashan Formation is best exposed in the Zhaogezhuang Section near Tangshan, Hebei Province, where it consists of a 160 m sequence of a thick-bedded lower limestone member and an upper dolomite member (Chen Xu *et al.*, 1995) that conformably overlies the Yeli (Yehli) Formation of Tremadocian age and is overlain by the Beianzhuang Formation of the

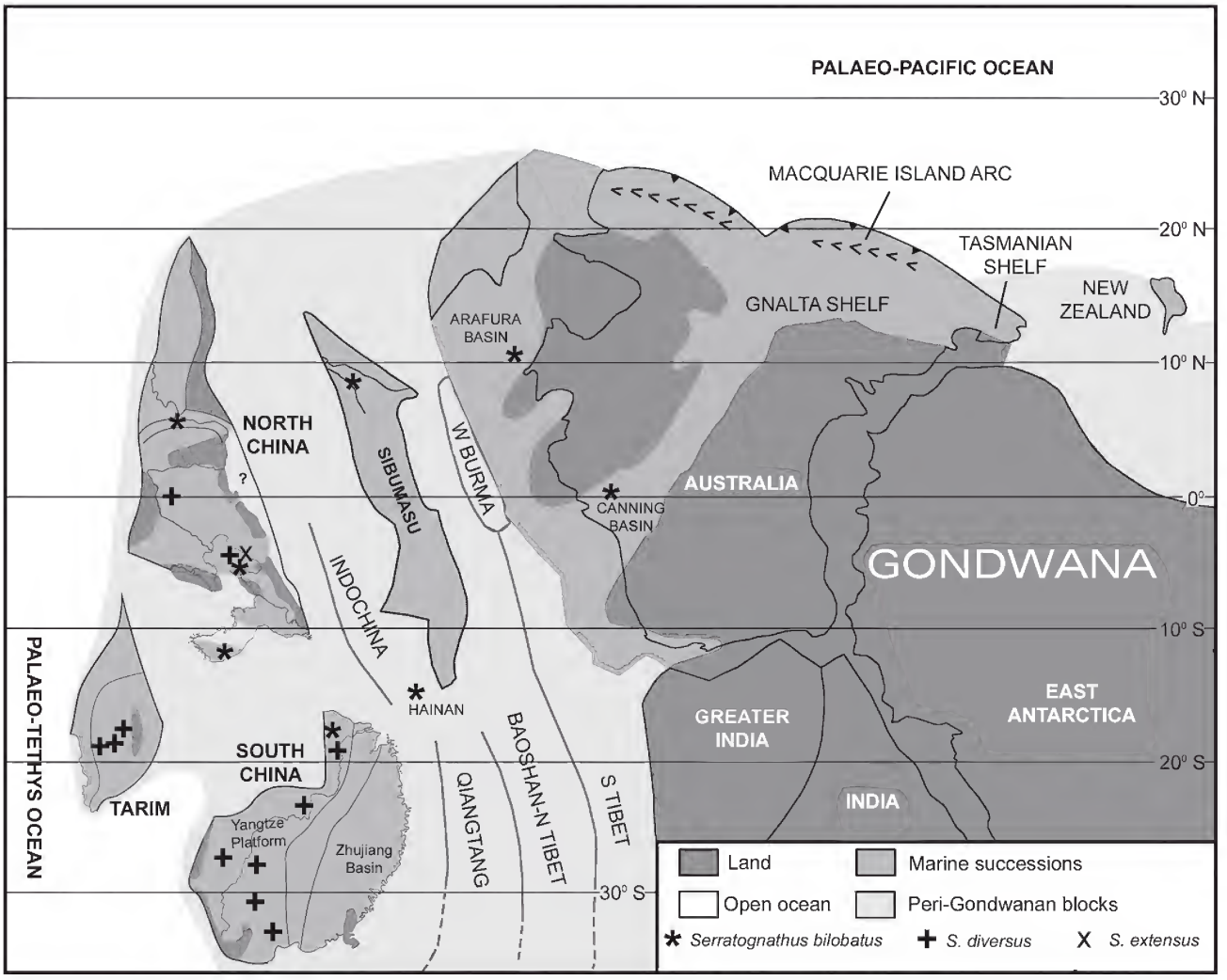

Fig. 3. Early Floian palaeobiogeographic reconstruction of eastern Gondwana (after Nicoll *et al.*, 1993; Webby *et al.*, 2000; Huang *et al.*, 2000).

late Floian to Dapingian age. An *et al.* (1983) subdivided the formation into four conodont biozones (in ascending order): (*1*) *Scalpellodus tarsus* Biozone; (*2*) *Serratognathus bilobatus* Biozone; (*3*) *Serratognathus extensus* Biozone; and (*4*) *Paraserratognathus paltodiformis* Biozone. The *S. bilobatus* Biozone is confined to the lower part of the Liangjiashan Formation with a total thickness of 30 m in the Zhaogezhuang Section; the overlying *S. extensus* Biozone ranges through the middle part of the formation with a total thickness of 50 m (An *et al.*, 1983, p. 26).

In the Honghuayuan Formation (the coeval strata on the Yangtze Platform of South China), *S. bilobatus* is rare and has been reported only from the Lower Yangtze Valley (An & Ding, 1982, 1985). A closely related species, *S. diversus*, is dominant in the fauna. Recent studies (Zhen *et al.*, in press *a*) of the conodonts from the Honghuayuan Formation at its type locality and several other sections in Guizhou resulted in the recognition of three conodont biozones in the Formation (in ascending order): *Triangulodus bifidus* Biozone, *Serratognathus diversus* Biozone and *Prioniodus honghuayuanensis* Biozone. In the type section of the Honghuayuan Formation, *S. diversus* is confined to an interval of 13.5 m in the middle part of the Formation which is correlated to the upper *P. proteus* Biozone of the Balto-Scandian succession (Zhen, 2007, Zhen *et al.* in press *a*).

When correlating the conodont fauna from the Emanuel Formation and the lower Gap Creek Formation with well-studied Balto-Scandian and North America Mid-continent conodont successions, McTavish (1973, p. 31) was puzzled by the fact that Balto-Scandian Lower Ordovician successions were condensed, while North America Mid-continent successions, although with "comparable thickness to the Emanuel Formation" had faunas "of limited value for precise age determination". At the time, he did not attribute these faunal differences and difficulties in correlation to either ecological or biogeographical reasons. It is now understood that distribution of conodont animals was largely controlled by the water temperature and the water depth of their habitats (see Zhen & Percival, 2003). Higher resolution of the faunal correlation can only be achieved by comparing faunas from the same biogeographical province and Domain or at least from the same realm, otherwise ecological and biogeographical overprints should be removed or discounted when comparing faunas from different biogeographical settings.

A restricted distribution of *Serratognathus* in eastern Gondwana (Fig. 3) strongly supports the concept that the so-called "Australasian Province" became evident in the latest Tremadocian and early Floian, and persisted through

most of the Ordovician (Nowlan *et al.*, 1997; Zhen *et al.* in Webby *et al.*, 2000). Restriction of *S. diversus* primarily to the South China and the Tarim plates also indicates a closer biogeographic relationship between these two Chinese plates in the early Floian, and agrees with the recent biogeographic analysis based on the trilobite geographical and stratigraphical distribution data from the Chinese Cambrian (Zhou *et al.*, 2008) and Ordovician (Zhou & Zhen, 2008). Trilobite data (Zhou & Zhen, 2008; Zhou *et al.*, 2008) suggested that a broad undifferentiated biogeographic entity persisted in the Chinese plates and terranes positioned in eastern Gondwana from Cambrian to Tremadocian time, and became more diversified in the early Floian when two subprovinces (North China and South China) could be recognized (Zhou *et al.*, 2008, fig. 2). Trilobite distributional patterns and sharing of several endemic forms also support a closer biogeographic tie between Australia and North China (Choi *et al.*, 2001; Zhou & Zhen, 2008; Zhou *et al.*, 2008).

Material and methods

All photographic illustrations shown in Figs 4 to 16 are SEM photomicrographs captured digitally (numbers with the prefix IY are the file names of the digital images). Conodont specimens for this study are from three samples from the Emanuel Formation that bear *S. bilobatus*. Both WCB705/133 and WCB705/243 are from Section WCB 705 measured by following the line of the type section (Guppy & Öpik, 1950; Grid Ref. for base: 18°39'50"S 125°54'00"E; and top: 18°39'12"S 125°55'05"E), and sample 161–166 m is from a drillhole (BHP/PDH, grid ref. 18°40'30"S 125°33'00"E, from the middle part of the Emanuel Formation, see Nicoll *et al.*, 1993) in the northern margin of the Canning Basin. Figured specimens bearing the prefix CPC are housed in the Palaeontology Collection of Geoscience Australia in Canberra. Those bearing the prefix "AM F" (Figs 12–14) are deposited in the collections of the Palaeontology Section at the Australian Museum, Sydney, and were collected from the Honghuayuan Formation in Guizhou (see Zhen *et al.* in press a for sampling locations and stratigraphic details). Several species documented herein only by illustration are rare in the collection [*Cornuodus* sp. (Fig. 4G–L), gen. et sp. indet. A (Figs 8L–O, 10Y), *Nasusgnathus dolonus* (An, 1981) (Fig. 10S–U), *Paltodus* sp. (Fig. 10X), *Protoprioniodus simplicissimus* McTavish, 1973 (Fig. 6M–R), gen.sp. indet. B (Fig. 10W), and *Triangulodus bifidus* Zhen in Zhen *et al.*, 2006 (Fig. 15I–K)] or those which are discussed adequately elsewhere [*Bergstroemognathus extensus* (Graves & Ellison, 1941) (see Zhen *et al.*, 2001; Fig. 4A–F), *Lissoepikodus nudus* Nicoll & Ethington, 2004 (see Nicoll & Ethington, 2004; Fig. 10L–R), and *Stiptognathus borealis* (Repetski, 1982) (see Ethington *et al.*, 2000; Fig. 15A–H)]. Conodont terminology and notation employed in this contribution are conventional as defined in Treatise Part W (Clark *et al.*, 1981), except for the M elements (makellate), whose orientation, morphology and the terminology was introduced by Nicoll (1990, 1992).

Systematic palaeontology

Phylum Chordata Balfour, 1880

Class Conodonta Pander, 1856

Acodus Pander, 1856

Diaphorodus Kennedy, 1980: 51.

Type species. *Acodus erectus* Pander, 1856.

Remarks. The name *Acodus*, although widely cited in Ordovician conodont literature, has been a subject of debate and has remained one of the most controversial conodont genera for many years. As its type species *A. erectus* was poorly known, Kennedy (1980) regarded *Acodus* as a *nomen dubium*, and this view was accepted by several subsequent workers (e.g., Sweet, 1988), while others (e.g., Lindström in Ziegler, 1977; Ji & Barnes, 1994; Zhen *et al.*, 2004) retained *Acodus* as a valid genus, but with varying definitions.

During the late Tremadocian to early Floian, conodonts evolved rapidly and experienced the greatest diversification event in their evolutionary history of some 300 million years. Several important clades, particularly the Prioniodontida, evolved from forms previously gouped with *Acodus*. Understanding of the apparatus composition and structure of *Acodus* and related taxa is crucial in depicting the phylogenetic relationships and evolutionary history of these related clades (Stouge & Bagnoli, 1999). Therefore, a narrower rather than broader generic concept is needed for *Acodus*, which is restricted herein to forms with the same apparatus composition and structure as *Prioniodus* but typically consisting of adenticulate elements.

Recent study by Nicoll & Ethington (2004) shows that Oepikodontidae diverged from the main clade of Prioniodontoidea in the late Tremadocian through an adenticulate stage represented by *Lissoepikodus* (recognized in the Emanuel Formation), and supports the hypothesis that both Prioniodontoidea and Balognathoidea might have evolved from a common ancestor (Stouge & Bagnoli, 1999), most likely *Acodus* (= *Diaphorodus* + "*Acodus*" *deltatus* of Stouge & Bagnoli, 1999).

As Pander's type specimens of the genotype, *A. erectus*, are lost, our current understanding of *Acodus* is largely based on several subsequent works on *A. deltatus* Lindström, 1955 and other related species documented by McTavish (1973),

[Fig. 4, caption continued]. (*G*), P element (short based), CPC39796, inner lateral view (IY129-024). *H–J*, Sa element; (*H*), CPC39797, lateral view (IY129-009); (*I*), CPC39798, lateral view (IY129-11); (*J*), CPC39799, basal view (IY129-014). (*K*), P element (short based), CPC39800, inner lateral view (IY129-020). (*L*), Sb element, CPC39801, inner lateral view (IY129-018). *M–R*, *Acodus*? *transitans* McTavish, 1973. *M–Q*, Pa element; M,N, CPC39802; (*M*), basal-outer lateral view (IY126-018); (*N*), outer lateral view (IY126-020). (*O*), CPC39803, inner lateral view (IY126-029). *P–R*, Sc element; P,Q, CPC39804; (*P*), outer lateral view (IY126-021); (*Q*), basal-outer lateral view (IY126-022); (*R*), CPC39805, outer lateral view (IY126-023). *S–X*, *Acodus deltatus*? Lindström, 1955. (*S*), M element, CPC39806, 161–166 m, posterior view (IY130-034); (*T*), Sb element, CPC39807, WCB705/243, outer lateral view (IY130-045); (*U*), Sd element, CPC39808, 161–166 m, inner lateral view (IY132-010); *V–X*, P element; V,W, CPC39809, 161–166 m; (*V*), anterior view (IY130-037); (*W*), inner lateral view (IY130-038); (*X*), CPC39810, 161–166 m, outer lateral view (IY130-028). Scale bars 100 μm.

Fig. 4. A–F, *Bergstroemognathus extensus* (Graves & Ellison, 1941). All from sample WCB705/243. (*A*), M element, CPC39790, posterior view (IY116-046). (*B*), Sa element, CPC39791, posterior view (IY116-047). (*C*), Sb element, CPC39792, inner lateral view (IY116-048). (*D*), Sc element, CPC39793, inner lateral view (IY116-049). (*E*), Pb element, CPC39794, inner lateral view (IY116-042). (*F*), Pa element, CPC39795, inner lateral view (IY116-043). *G–L*, *Cornuodus* sp. All from WCB705/243; …[continued on facing page]

Fig. 5. *A–F*, *Drepanodus arcuatus* Pander, 1856. All from sample WCB705/133. A,B, Sa element; (*A*), CPC39811, lateral view (IY126-002); (*B*), CPC39812, lateral view (IY126-003). *C,D*, Sd element; (*C*), CPC39813, inner lateral view (IY127-028); (*D*), CPC39814, inner lateral view (IY127-022). (*E*), Pb element, CPC39815, inner lateral view (IY126-001). (*F*), Pa element, CPC39816, outer lateral view (IY126-005). *G–P*, *Drepanoistodus* sp. cf. *D. nowlani* Ji & Barnes, 1994. (*G*), M element, CPC39817, WCB705/243, anterior view (IY129-005). *H,I*, Sa element; (*H*), CPC39818, WCB705/133, lateral view (IY126-004); (*I*), CPC39819, WCB705/133, lateral view (IY127-016). (*J*), Sb element, CPC39820, WCB705/133, inner lateral view (IY127-029). *K,L*, Sc element; (*K*), CPC39821, WCB705/133, outer lateral view (IY126-008); (*L*), CPC39822, WCB705/133, outer lateral view (IY129-027). (*M*), Sd element, CPC39823, WCB705/133, inner lateral view (IY127-030). *N,O*, Pa element; (*N*), CPC39824, WCB705/243, inner lateral view (IY129-025); (*O*), CPC39825, WCB705/243, outer lateral view (IY129-026). (*P*), Pb element, CPC39826, WCB705/243, outer lateral view (IY129-006). Scale bars 100 μm.

van Wamel (1974), Lindström (in Ziegler, 1977), Stouge & Bagnoli (1999), Zhen *et al.* (2003), Nicoll & Ethington (2004) and Zhen *et al.* (2005). McTavish (1973) described *A. deltatus* and several other species of *Acodus* from the Emanuel Formation of the Canning Basin, and suggested a seximembrate apparatus for *A. deltatus* including prioniodiform (= P of our interpretation), ramiform (trichonodelliform = Sa, gothodiform = Sb, cordylodiform = Sc, and tetraprioniodiform = Sd of our interpretation), and oistodiform (= M of our interpretation) elements. Based on the stratigraphical distribution and morphological changes of various *Acodus* species recognized in the Emanuel Formation, McTavish (1973, fig. 7) indicated that both *Prioniodus* and *Baltoniodus* might have evolved from *Acodus*. Some authors went even further by attributing *A. deltatus* to either *Prioniodus* (van Wamel, 1974) or *Baltoniodus* (Bagnoli *et al.*, 1988). In their revision of *A. deltatus*, Bagnoli *et al.* (1988) considered it to have a seximembrate apparatus without an Sa element, and included in this species some specimens from the Emanuel Formation illustrated by McTavish (1973). Subsequently Stouge & Bagnoli (1999) indicated that forms referred to *A. deltatus* by McTavish (1973), Ethington & Clark (1982) and

Repetski (1982) were actually species of *Diaphorodus* and not congeneric with their revised "*A.*" *deltatus*.

Kennedy (1980) proposed *Diaphorodus* as the replacement of *Acodus* and selected *A. delicatus* Branson & Mehl, 1933 as the type species. In his revision of this species from the Early Ordovician Jefferson City Formation of Missouri, he recognized a seximembrate apparatus including the following types of elements: oistodiform (= M of our interpretation) represented by the form species *Oistodus expansus* Branson & Mehl, 1933 (see Kennedy, 1980, pl. 1, figs 20–22); acontiodiform (= Sa herein; see Kennedy, 1980, pl. 1, figs 14–17); drepanodiform (= ?Sc herein) represented by the form species *Cordylodus simplex* Branson & Mehl, 1933 (see Kennedy, 1980, pl. 1, figs 9–11); distacodiform (= Sd herein) represented by the form species *Paltodus distortus* Branson & Mehl, 1933 (see Kennedy, 1980, pl. 1, figs 18, 19); acodiform (= Pa herein) represented by the form species *A. delicatus* Branson & Mehl, 1933 (see Kennedy, 1980, pl. 1, fig. 3); and oistodiform (= ?Pb herein) represented by the form species *Oistodus vulgaris* Branson & Mehl, 1933 (see Kennedy, 1980, pl. 1, figs 23–25). This multi-element species reconstruction is more or less agreeable with our current understanding of *Acodus*, except that the asymmetrical tricostate Sb element was absent in the type species of *Diaphorodus* defined by Kennedy (1980). However, Stouge & Bagnoli (1999) considered both *Diaphorodus* and *Acodus* (represented by "*Acodus*" *deltatus*) as valid genera. According to their illustrations of both *Diaphorodus* sp. A from the Cow Head Group of western Newfoundland (Stouge & Bagnoli, 1999, pl. 1, figs 1–7) and "*A.*" *deltatus* from the Köpingsklint Formation of Öland (Bagnoli *et al.*, 1988; Stouge & Bagnoli, 1999, text-fig. 2), both *Diaphorodus* with a septimembrate apparatus and *Acodus* with a seximembrate apparatus have a nearly identical species apparatus and element morphology, except there is no Sa element for "*A.*" *deltatus*. As argued by Zhen *et al.* (2005, p. 306), we prefer to retain *Acodus* as a valid genus and consider *Diaphorodus* tentatively as a junior synonym of *Acodus* pending further studies of these and other closely related forms.

Acodus deltatus? Linström, 1955

Fig. 4S–X

Acodus deltatus deltatus Linström.—McTavish, 1973: 39, pl. 1, figs 1–9, 12–14, text-fig. 3p–t.

Material. 209 specimens from three samples (Table 1).

Remarks. By assigning the Emanuel material to *Acodus deltatus* Lindström, 1955, McTavish (1973) defined *A. deltatus* as having a seximembrate apparatus. However, in a later revision of this Baltic species, Bagnoli *et al.* (1988) suggested that only some illustrated specimens referred to *A. deltatus deltatus* by McTavish (1973) might be doubtfully assignable to *A. deltatus*. Stouge & Bagnoli (1999) further indicated that the Emanuel material referred to *A. deltatus* was not conspecific with the type specimens from Sweden. As revision of the *Acodus* species described by McTavish (1973) and other related coniform taxa occurring in the Emanuel Formation is still in progress and will be presented elsewhere, the currently material is only tentatively referred to *A. deltatus*.

Acodus? transitans McTavish, 1973

Fig. 4M–R

Acodus transitans McTavish, 1973: 41, 42, pl. 1, figs 10, 11, 15, 17, 19, 21, 24, text-fig. 3 m–o.

Material. Four specimens from three samples WCB705/133 (Table 1).

Remarks. *Acodus transitans* is characterized by having a number of small and rudimentary denticles on the posterior process of its P and S elements, and represents a transitional form between *Acodus* and *Prioniodus*. Only a small number of specimens were available in this study (Fig. 4M–R). A comprehensive revision of *Acodus* species from the Emanuel Formation will be undertaken in a separate contribution.

Drepanodus Pander, 1856

Type species. *Drepanodus arcuatus* Pander, 1856.

Drepanodus arcuatus Pander, 1856

Fig. 5A–F

Drepanodus arcuatus Pander, 1856: 20, pl. 1, figs 2, 4–5, 17, 30, ?31; Löfgren & Tolmacheva, 2003: 211–215, figs 2, 3A–C, E–H, 5K–V, 6M–U, 7H–N, 8A–G (*cum syn.*); Zhen *et al.*, 2004: 52–53, pl. 3, figs 1–12; Zhen *et al.*, in press a: fig. 5A–N (*cum syn.*).

Material. 95 specimens from three samples (Table 1).

Remarks. Recently revised as having a septimembrate apparatus (Löfgren & Tolmacheva, 2003), *D. arcuatus* is a pandemic species widely distributed in various environments from inner shelf to slope (or basinal) settings with a long stratigraphic range from the late Tremadocian to Late Ordovician. It is a fairly common species in the Emanuel with specimens generally larger in comparison with those of other taxa. The cusp of the Sa element varies from proclined (Fig. 5B) to reclined (Fig. 5A), the Sd element has a twisted cusp and inwardly flexed anterobasal corner (Fig. 5C, D), the Pb element is characterized by having a strongly reclined cusp and a more or less square base in lateral view with basal margin curved into a right angle, and the Pa element bears a flared base with a shallower basal cavity (Fig. 5F). The symmetrical Sa element with a proclined cusp (Fig. 5B) is identical with the neotype and other illustrated specimens from western Russia and Sweden (Löfgren & Tolmacheva, 2003, fig. 3A, B, fig. 6O), and from the Honghuayuan Formation of Guizhou (Zhen *et al.*, in press a, fig. 5B). The illustrated Sd, Pb and Pa elements are also comparable with those illustrated by Löfgren & Tolmacheva (2003) from Russia (fig. 3E–G) and Sweden (fig. 5O,V), and those from the Honghuayuan Formation of Guizhou (Zhen *et al.*, in press a, fig. 5I, 5L, 5N).

Fig. 6. *A–F*, *Paracordylodus gracilis* Lindström, 1955. All from sample WCB705/243. (*A*), M element, CPC39827, anterior view (IY116-050). *B–E*, S elements; B–C, CPC39828, (*B*), inner lateral view (IY116-051); (*C*), close up showing chevron-shaped pattern of striae adjacent to anterior margin (IY126-052); (*D*), CPC39829, inner lateral view (IY126-053); (*E*), CPC39830, outer lateral view (IY126-054); (*F*), P element, CPC39928, outer lateral view (IY116055). *G,H,L*, *Prioniodus adami* Stouge & Bagnoli, 1988. G,H, Pa element, CPC39831, WCB705/243, (*G*), antero-outer lateral view (IY118-018); (*H*), outer lateral view (IY118-019). (*L*), Sa element, CPC39832, WCB705/243, posterior view (IY128-021). *M–R*, *Protoprioniodus simplicissimus* McTavish, 1973. All from sample WCB705/243. M, N, Sc element; (*M*), CPC39833, outer lateral view (IY118-020); (*N*), CPC39834, inner lateral view (IY118-030). *O,P*, Pa element, CPC39835, (*O*), inner lateral view (IY118-025); (*P*), upper-outer lateral view (IY118-023). *Q,R*, M element; (*Q*), CPC39836, anterior view (IY129-032); (*R*), CPC39837, posterior view (IY118-029). *I–K, S–V*, *Fahraeusodus adentatus* (McTavish, 1973). *I–K*, Sa element, CPC39838, WCB705/133, (*I*), lateral view (IY127-012); (*J*), anterior view, close up showing striae on the broad anterior face (IY127-011); (*K*), anterior view (IY127-010). (*S*), Sc element, CPC39839, 161–166 m, inner lateral view (IY130-001). (*T*), Sb element, CPC39840, 161–166 m, outer lateral view (IY130-002). *U,V*, Sd element, CPC39841, 161–166 m, (*U*), inner lateral view (IY130-005); (*V*), outer lateral view (IY130-006). Scale bars 100 μm unless otherwise indicated.

Drepanoistodus Lindström, 1971

Type species. *Oistodus forceps* Lindström, 1955.

Drepanoistodus sp. cf. *Drepanoistodus nowlani* Ji & Barnes, 1994

Fig. 5G–P

Drepanoistodus sp. cf. *Drepanoistodus nowlani* Ji & Barnes.—Zhen *et al.*, 2007b: 132–134, pl. 2, figs 1–21, pl. 3, figs 1–9 (*cum syn.*).

Material. 52 specimens from three samples (Table 1).

Remarks. The Emanuel specimens are comparable with those described from the Honghuayuan Formation of Guizhou as *D.* sp. cf. *D. nowlani* except for the less extended basal-anterior corner in the P elements (Fig. 5N–P).

Fahraeusodus Stouge & Bagnoli, 1988

Type species. *?Microzarkodina adentata* McTavish, 1973.

Fahraeusodus adentatus (McTavish, 1973)

Fig. 6I–K, S–V

?Microzarkodina adentata McTavish, 1973: 49, 50, pl. 3, figs 28, 33–35, 38–40, 42–44.
Fahraeusodus adentatus (McTavish).—Stouge & Bagnoli, 1988: 119, pl. 4, figs 12–14 (*cum syn.*); Lehnert, 1995:89, pl. 7, fig. 20A, 20B.

Material. Seven specimens from two samples (Table 1).

Remarks. Specimens representing the asymmetrical Sb element with a lateral costa on the outer lateral face (Fig. 6T), the strongly asymmetrical Sc element without a lateral costa on each side (Fig. 6S), and the asymmetrical Sd element with a costa on each side (Fig. 6U, V) were recovered in the two samples from the Emanuel Formation. A specimen representing the triform Sa element with a broad, nearly flat anterior face and with a sharp anterolateral costa on each side (Fig. 6I–K) is also assigned to this species. McTavish (1973) recognized a quinquimembrate apparatus including oistodiform (= M element), ozarkodiniform (= P element), trichonodelliform (= Sa element), cordylodiform (= Sc element), and tetraprioniodiform (= Sd element), and doubtfully assigned it to *Microzarkodina*. Stouge & Bagnoli (1988) proposed *Fahraeusodus* and selected *?M. adentata* as the type species. However, only a few specimens were recovered in the upper part of Bed 9 (*O. elegans* Biozone) of the Cow Head Group in Newfoundland, an interval stratigraphically slightly younger than the occurrence in the Emanuel Formation. The flat anterior face and edge-like anterolateral costa on each side of the Sa element are comparable with some specimens referred to *Fahraeusodus marathonensis* by Stouge & Bagnoli (1988, e.g., pl. 4, fig. 15) from the Cow Head Group.

Paracordylodus Lindström, 1955

Type species. *Paracordylodus gracilis* Lindström, 1955.

Paracordylodus gracilis Lindström, 1955

Fig. 6A–F

Oistodus gracilis Lindström, 1955: p. 576, pl. 5, figs 1–2.

Paracordylodus gracilis Lindström, 1955: p. 584, pl. 6, figs 11–12; Tolmacheva & Löfgren, 2000: 1117–1119, figs 5, 7; Tolmacheva & Purnell, 2002: 209–228, text-figs 1–10; Zhen *et al.*, 2004: p. 56, pl. 4, figs 19–22 (*cum syn.*).

Material. 35 specimens from sample WCB705/243 (see Table 1).

Remarks. *Paracordylodus gracilis* is one of the best known species in the Early Ordovician. The reconstructed apparatus initially was based on interpretation of collections of discrete specimens documented successively by Sweet & Bergström (1972), McTavish (1973), and van Wamel (1974). Their collective interpretations were confirmed nearly 30 years later by the *in situ* bedding plane assemblages (Tolmacheva & Löfgren, 2000; Tolmacheva & Purnell, 2002). Its species composition and structure based on numerous clusters from deep water radiolarian cherts in central Kazakhstan revealed important data about its evolutionary affinities (Tolmacheva & Purnell, 2002). *Paracordylodus gracilis* is widely distributed (see Tolmacheva & Löfgren, 2000; Tolmacheva & Purnell, 2002), ranging from the late Tremadocian (late *P. proteus* Biozone) to late Floian (mid *O. evae* Biozone). It was most common in the Open Sea Realm (from shelf edge to basinal setting), with typical examples reported in central Kazakhstan (Tolmacheva & Purnell, 2002) occurring as the dominant species making up 90–99% of the specimen numbers. It is present in similar deep water oceanic settings in cherts of turbiditic successions (Percival *et al.*, 2003), and also in allochthonous limestone or calcareous siltstone of slope settings (Zhen *et al.*, 2004) in eastern Australia on the margins of eastern Gondwana. *Paracordylodus gracilis* was also common in the shallow marine environments within the Cold Domain of the Shallow-Sea Realm, such as in the Balto-Scandian Province (Löfgren, 1978; Tolmacheva & Löfgren, 2000). Its occasional presence in outer shelf environments or more rarely in inner shelf habitats within Temperate or even Tropical domains can be attributed to up-welling of cold ocean currents.

Paroistodus Lindström, 1971

Type species. *Oistodus parallelus* Pander, 1856.

Paroistodus parallelus (Pander, 1856) emend. Löfgren, 1997

Fig. 7A–S

Oistodus parallelus Pander, 1856: 27, pl. 2, fig. 40.
Paroistodus parallelus (Pander).—Lindström, 1971: 47, fig. 8; Löfgren, 1997: 923–926, pl. 1, figs 1–12, 17, 21, text-fig. 5A–G (*cum syn.*); Albanesi in Albanesi *et al.*, 1998: 144, pl. 8, figs 27–30; Johnston & Barnes, 2000: 31–32, pl. 10, figs 10,11,15–17, 20; Tolmacheva *et al.*, 2001: fig. 4.12–4.13; Viira *et al.*, 2006: pl. 1, fig. 5.

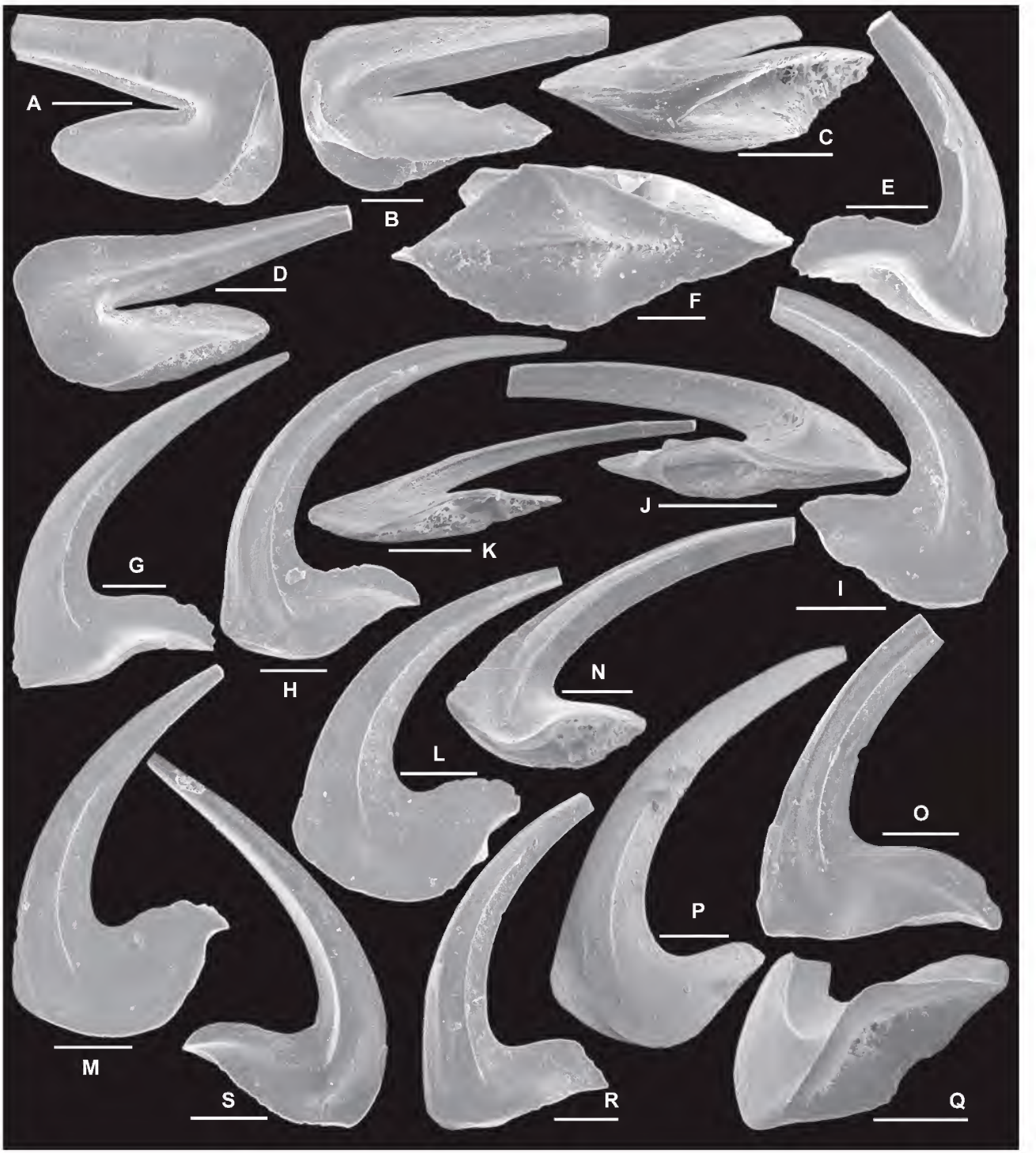

Fig. 7. *Paroistodus parallelus* (Pander, 1856). All from sample WCB705/133. *A–D*, M element; (*A*), CPC39842, anterior view (IY117-002); *B,C*, CPC39843, (*B*), anterior view (IY117-005); (*C*), basal view (IY117-006); (*D*), CPC39844, posterior view (IY117-008). *E–G*, Sa element; E,F, CPC39845, (*E*), lateral view (IY117-010), (*F*), basal view (IY117-011); (*G*), CPC39846, lateral view (IY117-009). *H–J*, Sb element; (*H*), CPC39847, outer lateral view (IY117-017); *I,J*, CPC39848, (*I*), inner lateral view (IY117-016), (*J*), basal view (IY117-018). *K–M*, Sc element; K,L, CPC39849, (*K*), basal view (IY117-014), (*L*), inner lateral view (IY117-013); (*M*), CPC39850, outer lateral view (IY117-012). *N,O*, Sd element; (*N*), CPC39851, inner-basal view (IY117-025); (*O*), CPC39852, outer lateral view (IY117-029). (*P*), Pb element; CPC39853, outer lateral view (IY132-020). *Q–S*, ?Pa element, (*Q*), CPC39854, basal view (IY117-036), (*R*), CPC39855, outer lateral view (IY117-030); (*S*), CPC39856, inner lateral view (IY117-034). Scale bars 100 μm.

Material. 457 specimens from three samples (Table 1).

Remarks. The species as revised by Löfgren (1997) possesses a septimembrate apparatus (including makellate M and drepanodiform or paroistodiform S and P elements), which can be distinguished from the other species of *Paroistodus* by having prominent lateral costae on the sides of its constituent elements. Zhen *et al.* (in press b) preferred to describe the S and P elements as paroistodiform in the *Paroistodus* species which show a sharp anterior costa extending basally into the basal cavity and forming a ridge-like structure (Zhen *et al.*, 2007b, p. 137) at the anterior end of the basal cavity. However this character is not shown in the material of the two *Paroistodus* species (similar to *Paroistodus* sp. recently documented from the Honghuayuan Formation in South China) reported herein from the Emanuel Formation, although the anterior part of base often exhibits a zone of recessive basal margin (Figs 7A–C, 8H). *Paroistodus parallelus* occurs abundantly in the Emanuel Formation, where it is found in association with *P. proteus* although the latter is rare (Table 1).

Paroistodus proteus (Lindström, 1955) emend. Löfgren, 1997

Fig. 8A–K

Drepanodus proteus Lindström, 1955: 566, pl. 3, figs 18–21, text-fig. 2a–f, j.
Paroistodus proteus (Lindström).—Löfgren, 1997: 922–923, text-figs 3H–N, 4L–AB (*cum syn.*); Zhen *et al.*, 2007b: 136, 137, pl. 5, figs 1–11 (*cum syn.*).

Material. 30 specimens from three samples (Table 1).

Remarks. *Paroistodus parallelus* is relatively rare in the Emanuel samples, and can be easily differentiated from associated *P. parallelus* mainly by lacking a prominent costa on the lateral faces. *Paroistodus proteus* was revised by Löfgren (1997) as having a septimembrate apparatus. After a review of previously reported occurrences of this species in the Honghuayuan Formation and other coeval stratigraphic units in South China and comparison with Baltic material of *P. proteus*, Zhen *et al.* (2007b) concluded that *Paroistodus* is represented in the Honghuayuan Formation by a rare form that they identified as *Paroistodus* sp. It differs from *P. proteus* in having a smooth lateral face without a carina and having a more open basal cavity which lacks the distinctive so-called paroistodiform character. The material from the Emanuel Formation is transitional between typical *P. proteus* from the late Tremadocian to Floian of Balto-Scandia and *Paroistodus* sp. from the Honghuayuan Formation of South China. It is comparable with *P. proteus* in having a prominent carina (Fig. 8A–E) or even a weak costa (Fig. 8J) on the lateral faces, but similar to *Paroistodus* sp. from the Honghuayuan Formation in lack of the paroistodiform feature. As mentioned above, absence of the paroistodiform character in species of *Paroistodus* co-occurring in the Emanuel Formation may indicate that this feature is caused by ecological adaption rather than as a phylogenetically significant trait for *Paroistodus*. Interestingly, *P. proteus* from the Emanuel Formation of Western Australia and from the Latorp Limestone and Tøyen Shale of Sweden and *Paroistodus* sp. from the Honghuayuan Formation of South China come from three contrasting ecological/sedimentological settings; they may represent three populations or subspecies of *P. proteus*. The typical latest Tremadocian and early Floian *P. proteus*-bearing successions in Sweden (e.g., Diabasbrottet area) were deposited in the outer shelf settings of the Cold Domain (Bergström *et al.*, 2004), and the mid-upper part of the Emanuel Formation might be largely deposited in deep subtidal settings, while the Honghuayuan Formation with *Paroistodus* sp. apparently represents typical shallow subtidal environments. Therefore, in consideration of the relationship between their morphological variation and their ecological/geographical distributions, the material from the Emanuel Formation is considered as conspecific with type material of *P. proteus*, and *Paroistodus* sp. from the Honghuayuan Formation (Zhen *et al.*, 2007b) might be better treated as a separate subspecies of *P. proteus*.

Prioniodus Pander, 1856

Type species. *Prioniodus elegans* Pander, 1856.

Prioniodus adami Stouge & Bagnoli, 1988

Fig. 6G–L

Prioniodus sp. nov. C McTavish, 1973: 47, pl. 3, figs 4–6, ?11, 16, text-fig. 6f, g, i, ?j, k.
Prioniodus adami Stouge & Bagnoli, 1988: 132, 133, pl. 11, figs 5–13 (*cum syn.*); ?Albanesi *et al.*, 1998: 155, pl. 10, figs 1–3; Johnston & Barnes, 2000: 36, pl. 16, figs 9, 10, 13–16, 19; Pyle & Barnes, 2002: 110, pl. 26, figs 19–21.

Material. Four specimens from two samples (Table 1).

Remarks. Based on a large collection from Bed 9 of the Cow Head Group of western Newfoundland, Stouge & Bagnoli (1988) established *P. adami* as having a septimembrate apparatus (pastinate Pa, and Pb, ramiform S and geniculate M elements), and also included in it the material from the Emanuel Formation that McTavish (1973), ascribed to *Prioniodus* sp. C except for the oistodiform element (his pl. 3, fig. 11, text-fig. 6j) which bears a short, adenticulate inner lateral process. *Prioniodus adami* is characterized by bearing small, closely-spaced denticles on the long posterior process of the S and P elements, as well as on the anterior and outer lateral processes of the P elements and the inner lateral process of the M element. The Pa element (Fig. 6G, H) from the Emanuel Formation is identical with those illustrated by McTavish (1973, pl. 3, figs 5, ?16), but exhibits less closely spaced denticles on the processes in comparison with the holotype (Stouge & Bagnoli, 1988, pl. 11, fig. 8). The M element from the Cow Head Group shows a long adenticulate outer lateral process and a long, denticulate inner lateral process with small, closely-spaced denticles, similar to those on the processes of the P and S elements, but no M element has been recovered from the samples of this study.

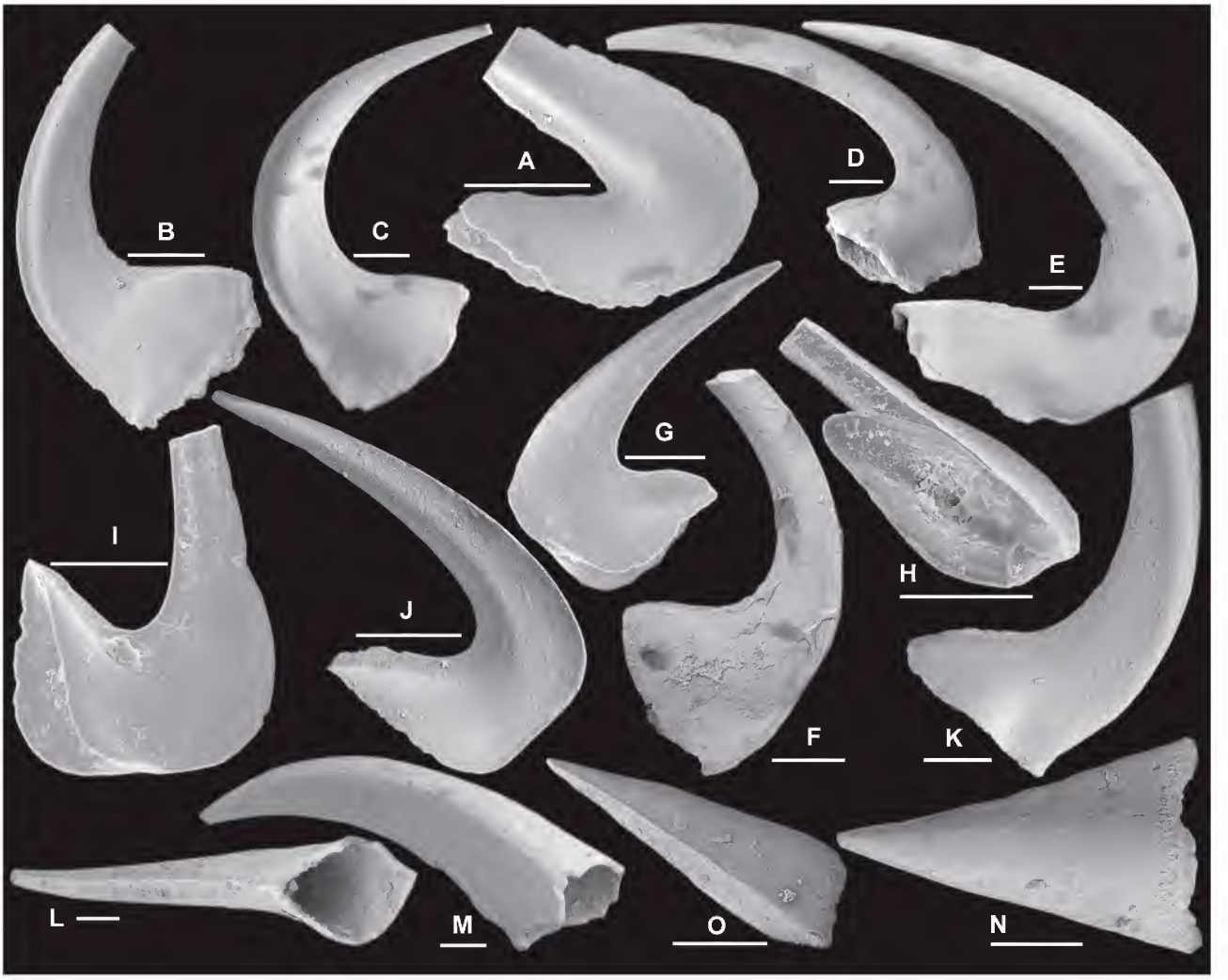

Fig. 8. *A–K*, *Paroistodus proteus* (Lindström, 1955). (*A*), M element, CPC39857, WCB705/133, posterior view (IY132-023). *B,C*, Sb element; (*B*), CPC39858, WCB705/133, inner view (IY132-022); (*C*), CPC39859, WCB705/133, outer lateral view (IY130-040). *D,E*, Sc element; (*D*), CPC39860, 161–166m, outer lateral view (IY130-025); (*E*), CPC39861, WCB705/133, inner lateral view (IY132-029). (*F*), Sd element, CPC39862, 161–166m, innrt lateral view (IY130-026). *G–J*, Pb element; (*G*), CPC39863, WCB705/133, outer lateral view (IY117-020); *H,I*, CPC39864, WCB705/133, (*H*), basal view (IY117-021), (*I*), inner lateral view (IY117-022); (*J*), CPC39865, WCB705/133, inner lateral view (IY130-043). (*K*), Sa element, CPC39866, WCB705/133, lateral view (IY130-41). *L–O*, gen. et sp. indet. A. All from sample WCB705/133. *L,M*, symmetrical element, CPC39867, (*L*), basal-posterior view (IY132-024), (*M*), lateral view (IY132-025). *N,O*, asymmetrical element, CPC39868, (*N*), outer lateral view (IY132-028), (*O*), anterior view (IY132-027). Scale bars 100 μm.

Protopanderodus Lindström, 1971

Type species. *Acontiodus rectus* Lindström, 1955.

Protopanderodus gradatus Serpagli, 1974

Fig. 9A–P

Protopanderodus gradatus Serpagli, 1974: 75, pl. 15, figs 5a–8b, pl. 26, figs 11–15, pl. 30, figs 1a–b; text-fig. 17; Zhen *et al.*, 2004: 56–57, pl. 5, figs 1–10 (*cum syn.*); Zhen & Percival, 2006: fig. 9A–C; Zhen *et al.*, in press a: fig. 8A–Q.

Material. 126 specimens from two samples (Table 1).

Remarks. *Protopanderodus gradatus* is common in one (WCB705/243) of the samples studied from the Emanuel Formation. This material is identical with the types described from the San Juan Formation (Early Ordovician) of Argentine Precordillera (Serpagli, 1974), and those recently documented from the Honghuayuan Formation of Guizhou, South China (Zhen *et al.*, in press a, fig. 8A–Q). An additional element (Fig. 9J–P) bearing a more compressed cusp and a less extended base with a rounded basal margin has also been recognized in the Emanuel material. It also shows rather prominent striation in the area immediately anterior to the lateral costa, and a weakly developed chevron-shaped pattern of striae adjacent to the anterior margin (Fig. 9K, O). As these distinctive characters are not observed in the other elements of *P. gradatus*, it is tentatively assigned herein to the M position of *P. gradatus*. Some specimens bear rounded holes of about 3–4.5 μm in diameter, presumably representing the boring structure made by an unknown organism (Fig. 9O, P).

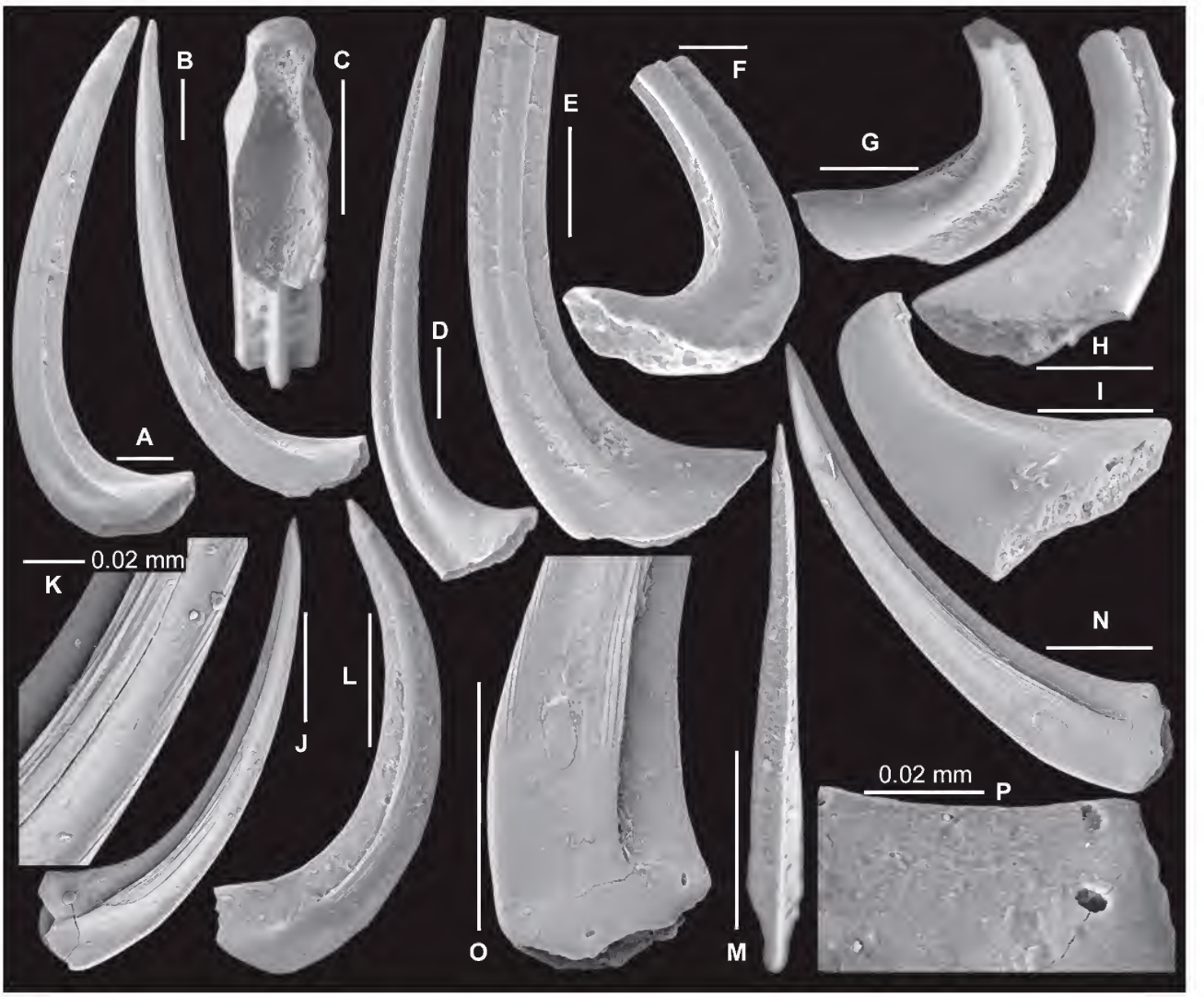

Fig. 9. *Protopanderodus gradatus* Serpagli, 1974. All from sample WCB705/243. *A–C*, Sa element; (*A*), CPC39869, lateral view (IY128-010); (*B*), CPC39870, lateral view (IY128-011); (*C*), CPC39871, basal view (IY128-008). *D–G*, Sc element; (*D*), CPC39872, inner lateral view (IY128-001); (*E*), CPC39873, inner lateral view (IY128-002); (*F*), CPC39874, basal-inner lateral view (IY128-005); (*G*), CPC39875, upper-inner lateral view (IY128-009). *H,I*, P element, CPC39876, (*H*), inner lateral view (IY128-019); (*I*), basal-outer lateral view (IY128-020). *J–P*, ?M element; J–K, CPC39877, (*J*), inner lateral view (IY129-037); (*K*), close-up inner lateral view, showing striae near the furrow and chevron-shaped pattern of striae adjacent to anterior margin (IY129-038); *L,M*, CPC39878, (*L*), outer lateral view (IY129-041); (*M*), anterior view (IY129-039); *N–P*, CPC39879, (*N*), inner lateral view (IY129-042); (*O*), close-up inner lateral view, showing striae near the furrow and chevron-shaped pattern of striae adjacent to anterior margin (IY129-043); (*P*), close up showing rounded boring hole on the surface (IY129-044). Scale bars 100 μm unless otherwise indicated.

Scolopodus Pander, 1856

Type species. *Scolopodus sublaevis* Pander, 1856.

Scolopodus houlianzhaiensis An & Xu in An *et al.*, 1983

Fig. 10A–K

Scolopodus rex houlianzhaiensis An & Xu in An *et al.*, 1983: 148, pl. 12, figs 23–27, text-fig. 11.7, 11.8; ?Ding, 1987: pl. 6, fig. 23; non Ding *et al.* in Wang, 1993: 205, pl. 14, figs 13–15.

Scolopodus houlianzhaiensis An & Xu.—Zhen *et al.*, in press a: fig. 9G–L.

Material. 19 specimens from three samples (Table 1).

Remarks. The multicostate Sa (symmetrical) and Sb (asymmetrical) elements of *Scolopodus houlianzhaiensis* show some resemblance to *S. quadratus*, but the distinctive Sc element has a strongly compressed cusp and lateral costae restricted to near the anterior margin (Fig. 10J, K). An & Xu (in An *et al.*, 1983) considered this species as a subspecies of *Scolopodus rex* Lindström, 1955, which is now regarded as a junior synonym of *Scolopodus striatus* Pander, 1856 (see Fåhraeus, 1982, Zhen *et al.*, 2004; Tolmacheva, 2006).

An & Xu (in An *et al.*, 1983) suggested a bimembrate apparatus including symmetrical and asymmetrical elements. Three morphotypes, representing symmetrical multicostate Sa, asymmetrical multicostate Sb, and strongly asymmetrical Sc elements, can be recognized among our Emanuel material. The Sa element (Fig. 10A–D) has a broad anterior face, five or six sharp costae on each side and a costa along the posterior margin, and is identical with the symmetrical element defined by An *et al.* (1983, pl. 12, figs 23–25) from the Liangjiashan Formation of North China. The Sb element

Fig. 10. *A–K*, *Scolopodus houlianzhaiensis* An & Xu in An *et al.*, 1983. All from sample 161–166 m. *A–D*, Sa element; *A,B*, CPC39880, (*A*), posterior view (IY130-011), (*B*), lateral view (IY130-010); *C,D*, CPC39881, (*C*), basal view (IY130-009), (*D*), lateral view (IY130-007). *E–G*, Sb element, CPC39882, (*E*), posterior view (IY130-017), (*F*), inner lateral view (IY130-016), (*G*), outer lateral view (IY130-018). *H–K*, Sc element; H,I, CPC39883, (*H*), posterior view (IY129-028), (*I*), inner lateral view (IY129-029); *J,K*, CPC39884, (*J*), outer lateral view (IY130-019), (*K*), inner lateral view (IY130-021). *L–R*, *Lissoepikodus nudus* Nicoll & Ethington, 2004. *L,M*, Sa element, CPC39885, WCB705/133, (*L*), upper view (IY127-002); (*M*), posterior view (IY127-003). *N,O*, Pb element; (*N*), CPC39886, WCB705/133, outer lateral view (IY127-014); (*O*), CPC39887, WCB705/133, outer lateral view showing weaker costa (IY127-006). *P,Q*, Sb element; (*P*), CPC39888, WCB705/243, basal view (IY118-016); (*Q*), CPC39889, WCB705/133, inner lateral view (IY126-034). (*R*), Sd element, CPC39890, WCB705/133, basal-inner lateral view (IY126-033). *S–U*, *Nasusgnathus dolonus* (An, 1981). All from sample WCB705/133. *S,T*, Sd element; (*S*), CPC39891, inner lateral view (IY127-008); (*T*), CPC39892, outer lateral view (IY127-007). (*U*), Sb element, CPC39893, WCB705/133, outer lateral view (IY127-005). (*V*), ?*Protoprioniodus simplicissimus* McTavish, 1973. Sb element, CPC39894, WCB705/243, outer lateral view (IY129-035). (*W*), gen. et sp. indet. B. Sa element, CPC39895, WCB705/133, posterior view (IY126-036). (*X*), *Paltodus* sp. M element, CPC39896, WCB705/133, posterior view (IY126-014). (*Y*), gen. et sp. indet. A. Symmetrical stout element, CPC39897, WCB705/133, lateral view (IY127-034). Scale bars 100 μm unless otherwise indicated.

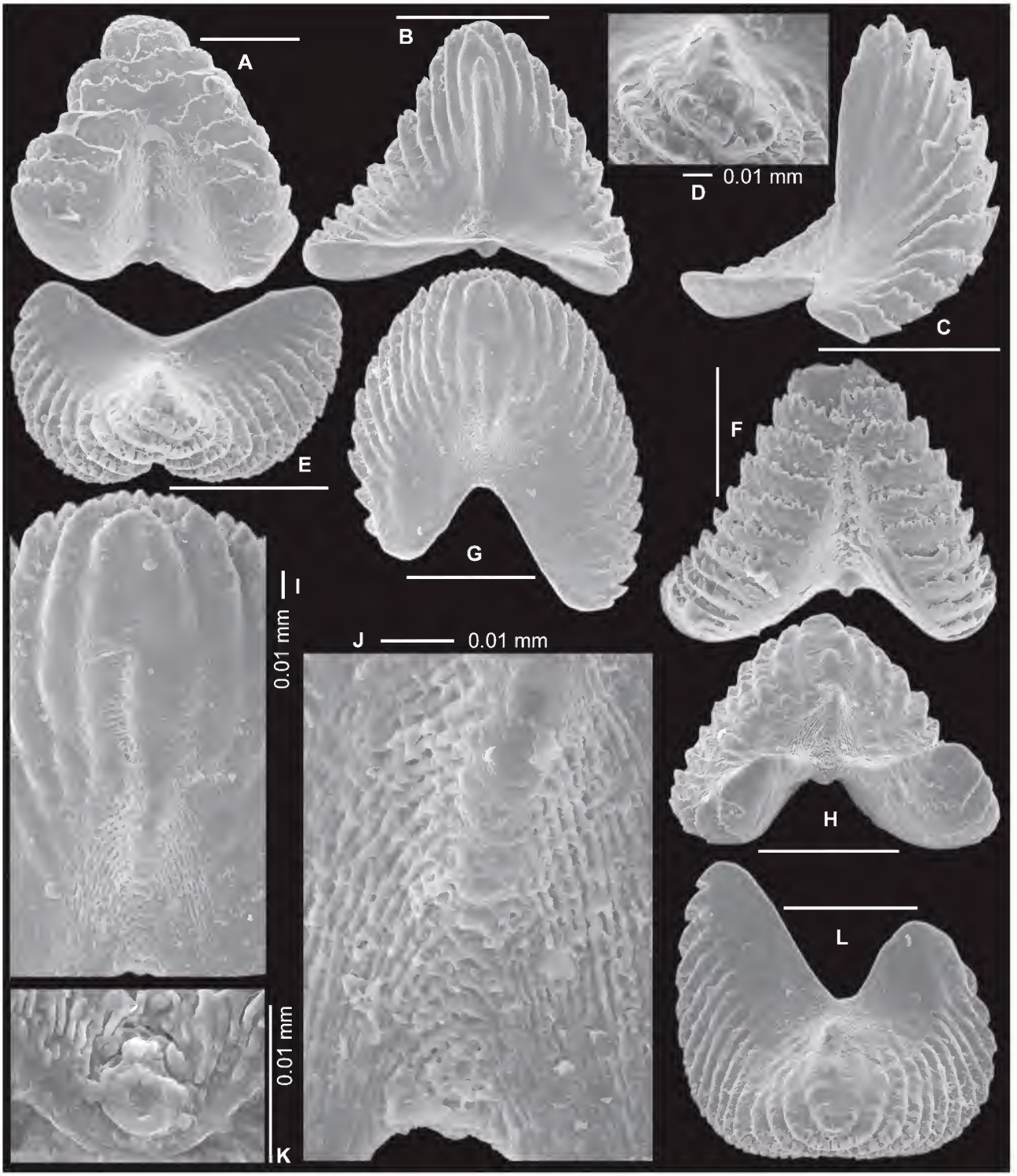

Fig. 11. *Serratognathus bilobatus* Lee, 1970. (*A*), Sa element, CPC39898, 161–166 m, anterior view (IY116-041). *B–F*, Sb element; *B–E*, CPC39899, WCB705/133, (*B*), posterior view (IY116-002), (*C*), outer lateral view (IY116-006), (*D*), upper view showing the tip of the cusp (IY116-012), (*E*), upper view (IY116-011); (*F*), CPC39900, WCB705/133, anterior view (IY116-028). *G–L*, Sc element, CPC39901, WCB705/133, (*G*), posterior view (IY116-013), L, upper view (IY116-023), (*H*), basal-posterior view (IY116018), (*I*), posterior view of the cusp (IY116-014), (*J*), posterior view, close up showing fine striae (IY116-015), (*K*), basal view showing ring-like basal node (IY116-022). Scale bars 100 μm unless otherwise indicated.

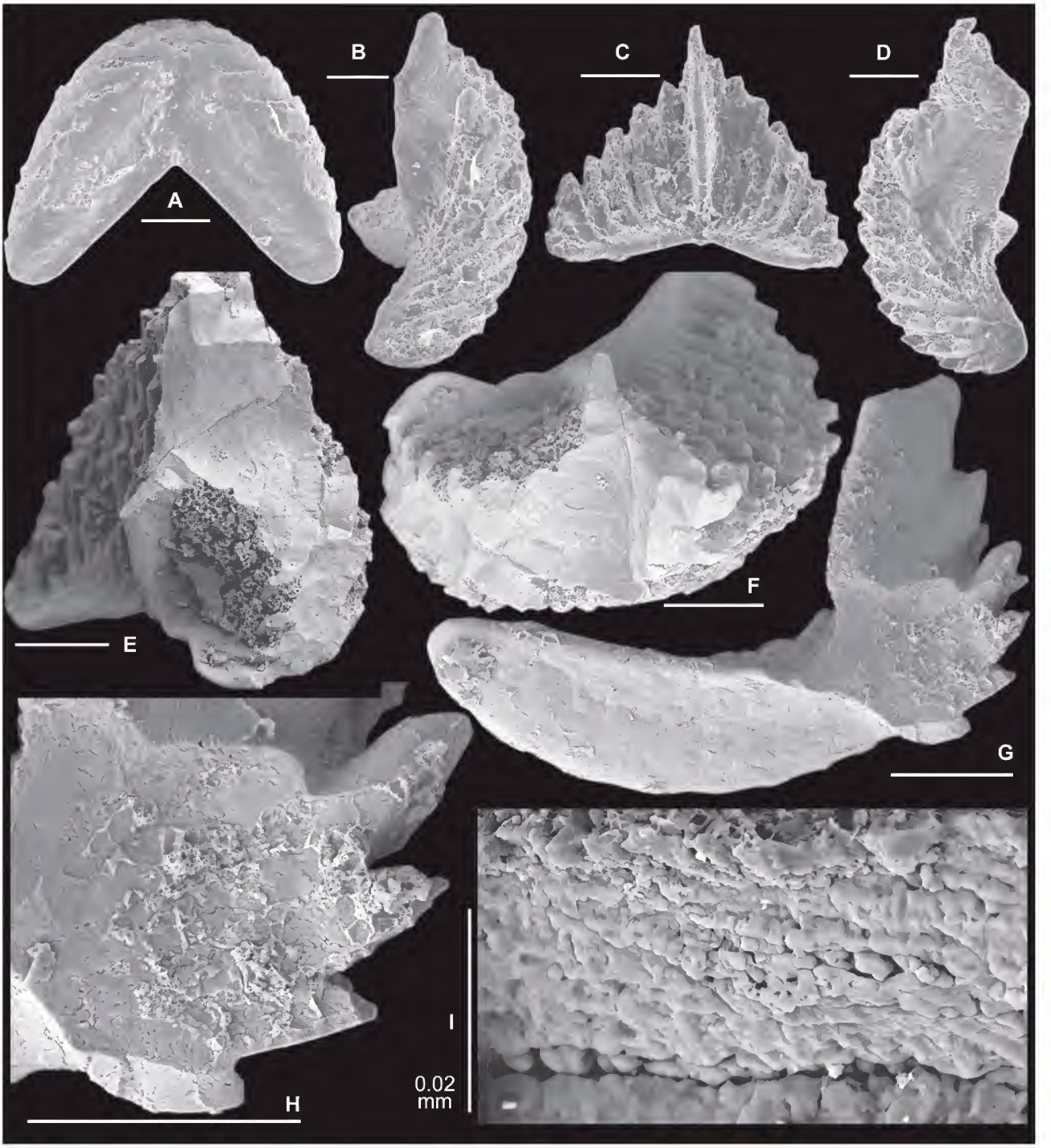

Fig. 12. *Serratognathus diversus* An, 1981. All from the Honghuayuan Formation in Guizhou. *A–C*, Sa element; (*A*), AM F.135048, THH7, anterobasal view (IY119-004); (*B*), AM F.135044, THH7, lateral view (IY119-002); (*C*), AM F.135047, THH10, posterior view (IY119-040). (*D*), Sb element, AM F.135049, THH7, outer lateral view (IY119014); *E–H*, broken specimens showing overlapping laminar layers on the surface of breakage. *E,F*, Sb element, AM F.135815, THH7, (*E*), postro-lateral view (IY133-035), (*F*), upper view (IY133-037); *G,H*, Sc element, AM F.135816, THH9, (*G*), inner lateral view (IY133-040), (*H*), close up showing the surface of breakage (IY133-041); (*I*), Sc element, AM F.135817, YTH10, showing the partition between laminar layers and the fine laminar structure within each laminar layer (IY133-033). Scale bars 100 μm unless otherwise indicated.

[Fig. 13 caption continued]… *G,H*, Sb element, AM F.135823, WHC36, (*G*), antero-outer lateral view, bearing 10 laminar layers (IY133-013), (*H*), close up showing denticles along anterior margin of each laminar layer (IY133-014). *I,J*, Sc element, AM F.135824, WHC36, (*I*), antero-outer lateral view, bearing 17 laminar layers (IY133-006), (*J*), posterior view (IY134-001). *K, L*, Sc element, AM F.135825, THH12, (*K*), anterior view, bearing 20 laminar layers (IY133-044), (*L*), posterior view (IY134-029). (*N*), Sc element, AM F.135826, WHC35, close up showing the small ring-like node representing the initial stage of the element (IY134-014). (*O*), Sc element, AM F.135817 (same specimen as Fig. 12I), YTH10, close up showing the rounded pit-like initial stage of the element (IY133-028). Scale bars 100 μm, unless indicated otherwise.

Fig. 13. *Serratognathus diversus* An, 1981. All from the Honghuayuan Formation in Guizhou. Showing size variation; A–*E,G,I,K* and *M* are magnified equally. (*A*), Sb element, AM F.135818, AFI983A, anterior view, bearing six laminar layers (IY133-046). (*B*), Sb element, AM F.135819, THH10, anterior view, bearing six laminar layers (IY133-038). *C,M*, Sc element, AM F.135820, YTH5, (*C*), anterior view, bearing eight laminar layers (IY133-024), (*M*), posterior view (IY134-019). (*D*), Sa element, AM F.135821, AFI986, upper-anterior view, bearing eight laminar layers (IY133-050). *E,F*, Sc element, AM F.135822, YTH4, (*E*), anterior view, bearing 10 laminar layers (IY133-021), (*F*), close up showing denticles along anterior margin of each laminar layer (IY133-022). …[continued on facing page]

resembles the Sa, but is asymmetrical with a more convex outer lateral face (Fig. 10E–G). The Sc element is identical with the asymmetrical element represented by the holotype of the species from the Liangjiashan Formation of North China (An *et al.*, 1983, pl. 12, fig. 26) with a convex outer lateral face and concave inner lateral face and with several costae (2 to 4) near the anterior margin (Fig. 10H–K). Zhen *et al.* (in press a, fig. 9G–L) reported the occurrence of this species in the Honghuayuan Formation in Guizhou. The Sc element recently illustrated from the Honghuayuan Formation in Guizhou (Zhen *et al.*, in press a, fig. 9G–I) shows a more compressed base, and the Sa element (Zhen *et al.*, in press a, fig. 9J–L) has the base less extended posteriorly, with costae on the lateral face more towards anterior.

Semiacontiodus Miller, 1969

Type species. *Semiacontiodus nogamii* Miller, 1969.

Semiacontiodus sp. cf. *Semiacontiodus cornuformis* (Sergeeva, 1963)

Fig. 15L–T

Scolopodus cornuformis Sergeeva.—An, 1987: 183, pl. 7, figs 10–11, 13–16; Ding *et al.* in Wang, 1993: 202, pl. 5, fig. 33; Zhen *et al.*, in press a: fig. 9D–F.

Material. 26 specimens from three samples (Table1).

Remarks. Three morphotypes of this species are recognized in the Emanuel samples representing a symmetry transition series including symmetrical Sa (Fig. 15L,M), asymmetrical Sb (Fig. 15N,O), and strongly asymmetrical and laterally more compressed Sc (Fig. 15P–T) elements. Although these specimens have relatively shorter bases, they otherwise resemble those of *S. cornuformis* (Sergeeva, 1963), which was revised as consisting of a septimembrate apparatus (Löfgren, 1999).

Serratognathus Lee, 1970

Type species. *Serratognathus bilobatus* Lee, 1970.

Serratognathus bilobatus Lee, 1970

Fig. 11A–L

Serratognathus bilobatus Lee, 1970: 336, pl. 8, figs 6, 7; Metcalfe, 1980: pl. 1, figs 16–19; An, 1981: pl. 2, fig. 26; An & Ding, 1982: pl. 5, fig. 25; An *et al.*, 1983: 149, pl. 16, figs 20–22, pl. 17, figs 1, 2; An, 1987: 189, 190, pl. 18, fig. 11; Ding, 1987: pl. 6, fig. 16; An & Zheng, 1990: pl. 7, fig. 13; Ding *et al.* in Wang, 1993: 207, pl. 20, fig. 5; Chen & Wang, 1993: fig. 2Q, 2U; Wang *et al.*, 1996: pl. 2, figs 1–7, 9; Nicoll & Metcalfe, 2001: fig. 6.19–6.22; Metcalfe, 2004: pl. 2, figs 9–10.

Material. Seven specimens from three samples (Table 1).

Diagnosis. Species of *Serratognathus* with a trimembrate apparatus, including symmetrical Sa, asymmetrical Sb, and strongly asymmetrical Sc elements; all elements semiconical in outline with fan-shaped array of small, closely spaced denticles along anterior and lateral edges of overlapping laminar layers; cusp small, posteriorly positioned and anterolaterally enclosed by up to 16 vertically overlapping laminar layers, which are anterobasally divided by a broad median groove into two lobe-like lateral processes; basal cavity absent.

Description. Trimembrate apparatus, including symmetrical Sa, asymmetrical Sb, and strongly asymmetrical Sc elements which form a symmetry transition series; each element semi-conical in outline, formed by upwardly overlapping layers, resembling a half-cut onion; composed of the cusp and a gently posterolaterally extended lobe-like lateral process on each side. Cusp small or indistinctive, weakly compressed laterally with a broad posterior face, and the anterior margin embedded in up to 16 surrounding overlapping layers, which are bordered by small, closely spaced denticles along the anterior and lateral margins. Discrete denticles surround the cusp in a semicircle, representing the anterolateral edge of each overlapping layer. Node-like denticles weakly developed on posterior face, may be absent towards the base (Fig. 11B, E, G, I); fine striae microstructure best developed on the posterior face in the area above the basal margin (Fig. 11 I, J). Denticulate anterior margin of each layer turned upwards. Basal face smooth, wide, and distally arched; crescentic in outline in basal view; bisected by anteroposteriorly directed median groove extending anterobasally to separate into two lobes underneath each lateral process. Basal cavity absent; basal end of the cusp represented by a small ring-like node (Fig. 11K), but in one specimen basal cavity represented by a small, shallow pit underneath the cusp (Fig. 11B).

Sa element symmetrical, outline crescentic in upper view with convex anterior face and concave posterior face, and tower-like in anterior view (Fig. 11A). Cusp small, located posteromedially with a short lobe-like process on each side, which extends posterolaterally; in anterior view, two processes separated anterobasally by a prominent rather deep median groove (Fig. 11A). Basal face smooth, bisected by the median groove into two symmetrical lobes.

Sb element (Fig. 11B–F) like Sa, but asymmetrical; inner lateral process shorter in posterior view (Fig. 11B), extending laterally with basal margin nearly horizontal; outer lateral process longer extending posterolaterally (Fig. 11C). Basal margin of the two processes forming an angle of 125° or more in the upper view (Fig. 11E). Basal face asymmetrical, with a longer lobe under outer lateral process and a shorter lobe under inner lateral process. One specimen (Fig. 11B) exhibits a small and shallow basal cavity.

Sc element (Fig. 11G–L) similar to Sb, but strongly asymmetrical with longer and more strongly posteriorly extended lateral processes. In upper view, the basal margins of the two lateral processes form a rather narrower angle of about 70–80° (Fig. 11G, L); outer lateral process longer (Fig. 11G, L).

Remarks. Lee (1970) illustrated two specimens of *Serratognathus bilobatus* from the Dumugol Formation of South Korea, with the figured holotype (Lee, 1970, pl. 8, fig. 7a–d) assignable to the asymmetrical Sb element defined herein and the other figured paratype (Lee, 1970, pl. 8, fig. 6) is a symmetrical Sa element. Both specimens are identical with those from the Emanuel Formation. *Serratognathus bilobatus* differs from *S. diversus* An, 1981 (Figs 12–14) from the Honghuayuan Formation of South China mainly in having a smaller, often indistinct, cusp (Fig. 11G, H).

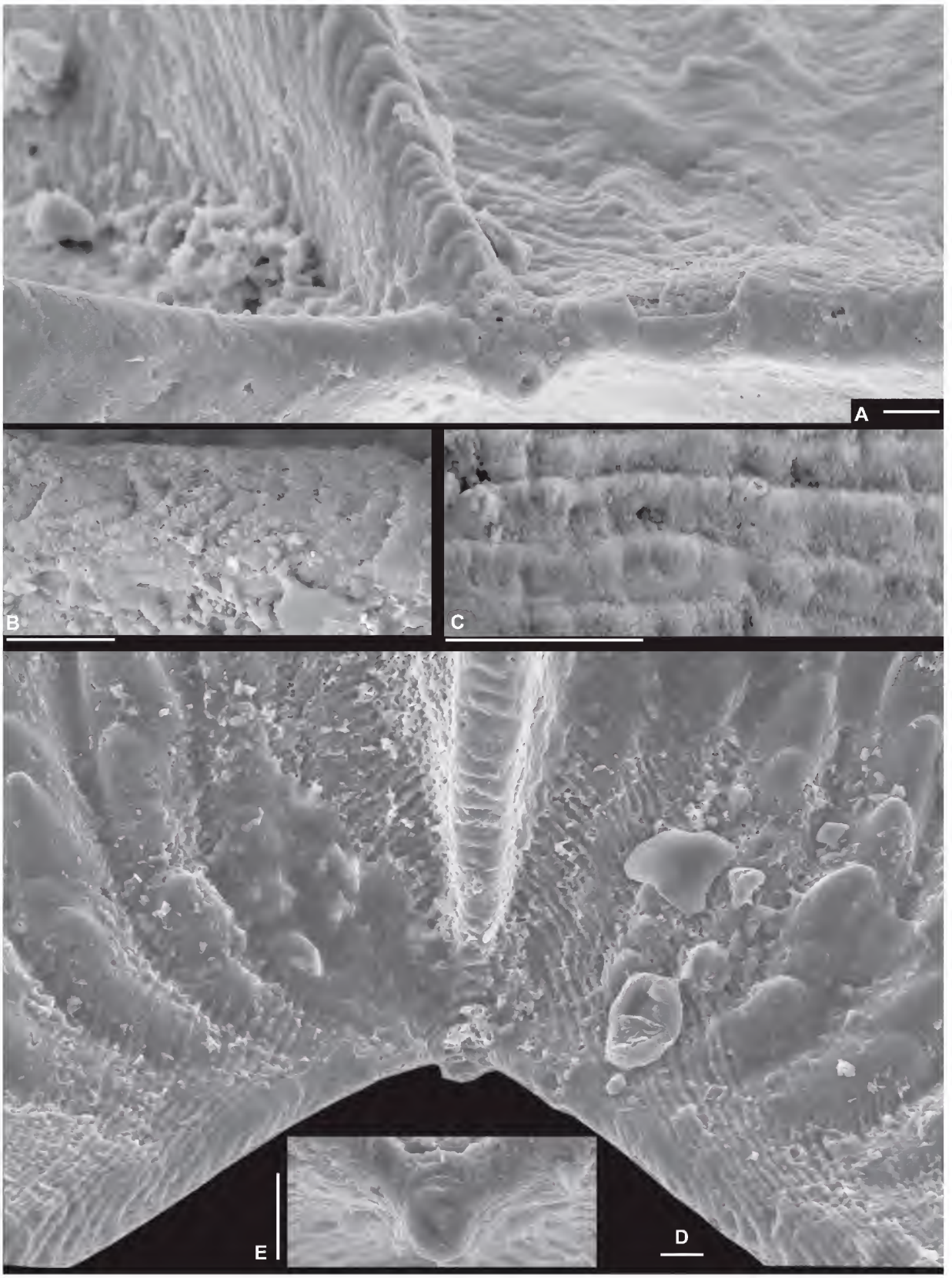

Fig. 14. *Serratognathus diversus* An, 1981. All from the Honghuayuan Formation in Guizhou. (*A*), Sb element, AM F.135050, THH7, basal-posterior view, showing fine growth laminar preserved on the lateral and posterior surfaces of the cusp (IY119-022). (*B*), Sc element, AM F.135825 (same specimen as Fig. 13K,L), THH12, close up showing growth laminar along the posterobasal margin (IY134-037). (*C*), Sc element, AM F.135816 (same specimen as Fig. 12G, H), THH9, closing up showing fine growth laminar on the posterior face (IY134-049). *D*,*E*, Sa element, AM F.135048, THH7, (*D*), close up showing fine growth laminar on the posterior face (IY119-006), (*E*), close up showing the small ring-like node representing the initial stage of the element (IY119-012). Scale bars 10 μm.

Fig. 15. *A–H*, *Stiptognathus borealis* (Repetski, 1982). (*A*), M element, CPC39902, WCB705/243, posterior view (IY129-033). *B–D*, Sa element; B,C, CPC39903, WCB705/243, (*B*), upper-posterior view (IY118-006), (*C*), upper-anterior view (IY118-007); (*D*), CPC39904, WCB705/243, upper view showing the cross section of the cusp (IY118-004). *E–G*, Sb element, E,G, CPC39905, WCB705/133, (*E*), basal-posterior view (IY117-041), (*G*), posterior view (IY117-039). (*F*), CPC39906, WCB705/243, basal view (IY118-015). (*H*), Pb element, CPC39907, WCB705/243, antero-inner lateral view (IY118-008). *I–K*, *Triangulodus bifidus* Zhen in Zhen *et al.*, 2006. Sd element, CPC39908, WCB705/133, (*I*), basal view (IY116-056), (*J,K*), posterolateral views (IY116-058, IY116-057). *L–T*, *Semiacontiodus* sp. cf. *S. cornuformis* (Sergeeva, 1963). *L,M*, Sa element, CPC39909, WCB705/133, (*L*), posterior view (IY126-027); (*M*), posterolateral view (IY126-028). *N,O*, Sb element; (*N*), CPC39910, 161–166 m, inner lateral view (IY132-012); (*O*), CPC39911, 161–166 m, outer lateral view (IY132-014). *P–T*, Sc element; *P–R*, CPC39912, 161–166 m, (*P*), inner lateral view (IY132-016); (*Q*), basal view (IY132-018); (*R*), outer lateral view (IY132-017). *S,T*, CPC39913, WCB705/133, (*S*), inner lateral view (IY127-018); (*T*), close up showing fine striae (IY127-019). Scale bars 100 μm unless otherwise indicated.

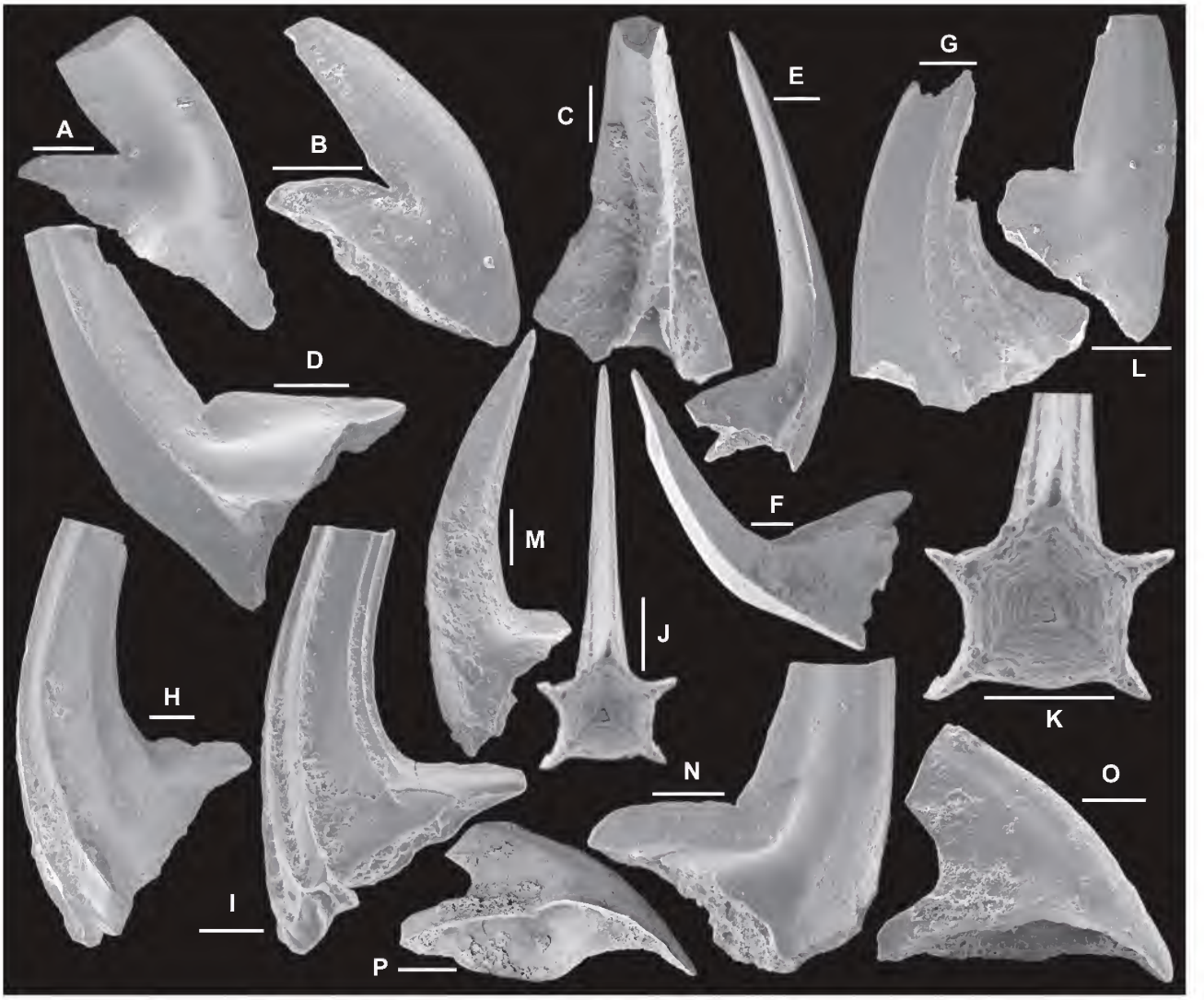

Fig. 16. *Tropodus australis* (Serpagli, 1974). *A,B*, M element; (*A*), CPC39914, WCB705/243, posterior view (IY128-032); (*B*), CPC39915, WCB705/243, anterior view (IY129-007). (*C*), Sa element, CPC39916, WCB705/243, posterior view (IY128-034). (*D*), Sb1 element (tricostate), CPC39917, WCB705/243, outer lateral view (IY128-033). *E,F*, Sb2 element (four costate); (*E*), CPC39918, WCB705/243, outer lateral view (IY128-038); (*F*), CPC39919, WCB705/243, inner lateral view (IY128-036). *G–I*, Sc element; (*G*), CPC39920, WCB705/243, outer lateral view (IY129-003); (*H*), CPC39921, WCB705/243, inner lateral view (IY129-022); (*I*), CPC39922, WCB705/243, inner lateral view (IY118-032). *J,K*, Sd element, CPC39923, WCB705/243, (*J*), basal view (IY118-033), (*K*), basal view close up showing the lamellar structure in the basal cavity (IY118-034). *L–N*, Pa element; (*L*), CPC39924, WCB705/243, outer lateral view (IY128-028); (*M*), CPC39925, WCB705/243, inner lateral view (IY128-022); (*N*), CPC39926, WCB705/243, inner lateral view (IY128-029). *O,P*, Pb element, CPC39927, WCB705/243; (*O*), outer lateral view (IY129-031), (*P*), basal view (IY129-030). Scale bars 100 μm.

Serratognathus diversus An, 1981

Figs 12–14

Serratognathus sp. A An *et al.*, 1981: pl. 1, fig. 10.
Serratognathus diversus An, 1981: 216, pl. 2, figs 23, 27, 30; Zhen *et al.*, in press a: figs 10A–K, 11A–K, 12D–M (*cum syn.*).
Serratognathus obliquidens Chen, Chen & Zhang, 1983: 136, pl. 1, fig. 18.
Serratognathus tangshanensis Chen, Chen & Zhang, 1983: 136–137, pl. 1, figs 14–17; Chen & Zhang, 1989: 223, pl.5, fig. 12.

Remarks. Both *Serratognathus obliquidens* and *S. tangshanensis* were erected as form species from the Honghuayuan Formation exposed in the Nanjing Hills (Chen *et al.*, 1983). We consider them to be junior synonyms of *S. diversus*, representing the asymmetrical elements (Sb + Sc) of our current notation.

Based on a large collection of *S. diversus* from the Honghuayuan Formation, Zhen *et al.* (in press a) recognized a trimembrate apparatus including symmetrical Sa, asymmetrical Sb and strongly asymmetrical Sc elements (Fig. 12). Material of *S. bilobatus* from the Emanuel Formation shows the same apparatus. Morphologically, *S. diversus* and *S. bilobatus* are closely comparable except that the former has a much more prominent, laterally compressed cusp. Their elements are resembling a half-cut onion with a posteriorly located cusp enveloped anterolaterally by numerous overlapping laminar layers (varying from 6 to 20, see Fig. 13). The upper margins of these laminae are progressively lower anterolaterally. Laminae are ornamented with

tooth-like denticles (Fig. 13) along their anterior and lateral margins, and by blunt node-like denticles along the posterior margins (Fig. 14D). Underneath each specimen is a wide, smooth, distally arched basal face (Fig. 12A, G), which is crescentic in outline and divided anteroposteriorly into two lobes (lateral processes; Fig. 13 A–E, K) by a broad, median groove. Typically a small ring-like node underneath the cusp represents the initial stage of the element (Figs 13N, 14E), without basal cavity.

Natural breakage surfaces on some of the specimens show these laminar layers to be tightly compacted (Fig. 12G, H) with partitions generally observed only near the edge of each layer (Fig. 12E–H). In most cases, no microstructure is observable on the surface of the breakage. However, some specimens show fine laminations (growth lamellae) formed by flattened crystallites (Fig. 12I).

Serratognathus extensus Yang in An *et al.*, 1983 differs from *S. diversus* in having a more robust cusp and a long, laterally extended process on each side. This species is similar to *S. diversus* and *S. bilobatus* in that the anterior face bears 2–3 rows of denticles that extend continuously from the end of one lateral process to the other, and in lack of a basal cavity. Yang's type material included 14 specimens from the Liangjiashan Formation in Hebei Province (An *et al.*, 1983, tables 6–7). An *et al.* (1983, p. 26) suggested that *S. extensus* might be directly evolved from *S. bilobatus*, and recognized the *S. extensus* Zone succeeding the *S. bilobatus* Zone in the Liangjiashan Formation.

Tropodus Kennedy, 1980

Chionoconus Smith, 1991: 22.

Type species. *Tropodus comptus* (Branson & Mehl, 1933).

Remarks. *Tropodus* Kennedy, 1980 is treated herein as a valid genus, having a rather different species apparatus as that of *Acodus*, particularly its S elements that exhibit a much wider variation characterized by the occurrence of multi-costate elements, and the P elements typically with weaker development of a lateral costa that may be represented by a broad carina. *Tropodus* was proposed to consist of a bimembrate apparatus (comprising comptiform and pseudoquadratiform elements) with *Paltodus comptus* Branson & Mehl, 1933 as the type species (Kennedy, 1980). Although the genus was originally defined as consisting of a symmetry transition series of elements bearing "three or more, prominent keel-like costae" (Kennedy, 1980, p. 65), both elements of his revised *T. comptus* have five costae, likely representing only part of a species apparatus. The comptiform element (= Sc herein) was represented by the form species *P. comptus*, an asymmetrical element with costate anterior and posterior margins, and with two costae on the outer face and one on the inner face (Kennedy, 1980, pl. 2, figs 21–24), and the pseudoquadratiform element (= Sd herein) by the form species *Scolopodus pseudoquadratus* Branson & Mehl, 1933, a symmetrical quinquicostate element with a broad anterior face and a costate posterior margin (Kennedy, 1980, pl. 2, figs 25–27).

The other species originally included in *Tropodus* was *Walliserodus australis* which was defined as consisting of a transitional series from tricostate to multicostate elements (Serpagli, 1974, p. 89). Kennedy (1980) admitted that "the two types of elements in *T. comptus* are very similar to two of the many morphologies of elements in *T. australis* (Serpagli, 1974)" although the latter presented "a multitude of variably costate forms." Serpagli (1974) originally defined a quinquimembrate apparatus for *T. australis* including asymmetrical tricostate (= Sb1 herein), asymmetrical quadricostate (= Sb2 herein), strongly asymmetrical, laterally compressed multicostate (= Sc herein) and a nearly symmetrical quinquicostate (= Sd) elements; Sa, P and M elements were originally not recognized in either species.

Based on material from the Cow Head Group of Newfoundland, Bagnoli *et al.* (1988) and Stouge & Bagnoli (1988) included P and M elements in the species apparatus of *Tropodus*. Stouge & Bagnoli (1988) also revised both *T. comptus* and *T. sweeti* (Serpagli, 1974), and suggested that *W. australis* proposed by Serpagli (1974) comprised elements belonging to both *T. comptus* and *T. sweeti*. As Smith (1991) correctly pointed out, distinguishing between S elements belonging to these species is rather uncertain, as Stouge & Bagnoli (1988) had included the holotype (tricostate element) of *W. australis* in the synonymy lists of both *T. comptus* and *T. sweeti*. However, the P elements they defined for *T. comptus* and *T. sweeti* show remarkable differences. The P elements of *T. comptus* illustrated from the Cow Head Group (Stouge & Bagnoli, 1988, pl. 16, fig. 2) and also from Utah (Ethington & Clark, 1982, text-fig. 22, pl. 11, figs 6, 7) are more or less scandodiform bearing a smooth, convex outer face and a concave inner face with a broad, prominent mid carina, while the P element of *T. sweeti* is a typical acodiform element with a prominent costa on one side (Serpagli, 1974, pl. 14, figs 13, 14, pl. 24, figs 8–10). Smith (1991) restricted *Tropodus* to Kennedy's original definition by including only costate elements in the species apparatus and proposed *Chionoconus* to accommodate those elements which Stouge & Bagnoli (1988) defined as the P elements of *T. comptus*.

Zhen *et al.* (2004) reported the occurrence of *T. Australis* (assigned to *T. comptus*) and *T. sweeti* from two samples within the Early Ordovician Hensleigh Siltstone in central New South Wales. The P and M elements of both these species are comparable with those described by Serpagli (1974) from the San Juan Formation of Precordilleran Argentina and by Stouge & Bagnoli (1988) from Newfoundland. However, Zhen *et al.* (2004), following Ji & Barnes (1994), applied a rather different concept for the S elements by including a symmetrical Sa element in the apparatuses. These studies also raised uncertainties about the definition of the constituent species of *Tropodus*. Firstly, if P elements of *Tropodus* are confined to "scandodiform" elements as Stouge & Bagnoli (1988) originally proposed, *T. sweeti* should be excluded from it. Secondly, although Kennedy (1980) suggested that *Triangulodus* consisted of hyaline elements, if *Tropodus* is considered as bearing "scandodiform" P elements, it would be very similar to *Triangulodus*, if it is not considered as a junior synonym of the latter. Among the specimens from the Hensleigh Siltstone, two types of P elements were recognized for *T. australis* (Zhen *et al.*, 2004). Both Pa and Pb elements

have a broad convex outer face and a concave inner face with a thin anterior margin curved inward. The lateral costa is weak, and may even be represented only as a broad carina on the inner side of the Pa element (Zhen *et al.*, 2004, pl. 1, figs 1, 3) which is comparable with those illustrated by Stouge & Bagnoli (1988, pl. 16, fig. 2)and those from the Emanuel Formation (Fig. 16L–P). However, the lateral costa is plainly evident in the Pb element (Zhen *et al.*, 2004, pl. 1, fig. 4). Similar variations among the P elements of *T. comptus* were also observed in the material from the St. George Group (Ji & Barnes, 1994). Therefore, *Tropodus* is defined herein as consisting of a geniculate M element, a series of highly variable S elements (in respect to the number of the costae), and acodiform P elements with a lateral costa on the inner side varying from weak to well developed.

Tropodus australis (Serpagli, 1974)

Fig. 16A–P

Walliserodus australis Serpagli, 1974: 89–91, pl. 19, figs 5a–10c, pl. 29, figs 8–15, text-figs 23, 24.
Tropodus australis (Serpagli).—Albanesi *et al.*, 1998: 151, pl. 13, figs 12–18.
Tropodus comptus australis (Serpagli).—Stouge & Bagnoli, 1988: 141, 142, pl. 16, figs 3–5; Löfgren, 1993: fig. 9: o, s, t; Lehnert, 1993: pl. 4, fig. 5; Lehnert, 1995: 129, 130.
Acodus comptus (Branson & Mehl, 1933).—Zhen *et al.*, 2004: 50, 51, pl. 1, figs 1–19.
Scolopodus ?rex Lindström.—Percival *et al.*, 1999: 13, fig. 8.9.
Tropodus ?sweeti (Serpagli).—Percival *et al.*, 1999: 13, fig. 8.10.

Material. 190 specimens from three samples (Table 1).

Remarks. Specimens from the Emanuel Formation are identical with those recovered from the Hensleigh Siltstone of central New South Wales (Zhen *et al.*, 2004, pl. 1, figs 1–19). Stouge & Bagnoli (1988) regarded *W. australis* as a subspecies of *T. comptus*. In the Emanuel Formation samples, only one species of *Tropodus*, *T. australis* is represented, exhibiting similar variation of the S elements (Fig. 16C–K) as was documented by Serpagli (1974), and the P elements (Fig. 16L–P) that are comparable with those described by Stouge & Bagnoli (1988) from the Cow Head Group of Newfoundland.

Tropodus australis differs from typical *T. comptus* of the North American Mid-continent (Kennedy, 1980; Ethington & Clark, 1982; Landing & Wesrop, 2006) mainly in having a strongly laterally compressed, muti-costate (Sc) element. Landing & Westrop (2006) documented *T. comptus* from the Fort Cassin (Early Ordovician, Floian) of northeastern New York, and defined it as consisting of a septimembrate apparatus including S, M and P elements, and also illustrated a scandodiform element as representing the Sc position (see Landing & Westrop, 2006, fig. 6.15). In the study of conodont faunas from the Jefferson City and other equivalent units in Oklahoma (Kindblade), Ethington (2009, per. com.) recognized the possible P elements of *T. comptus* and noticed their considerable difference from those of *T. australis* illustrated herein from the Emanuel Formation. He suggested that elements of *T. australis* tended to be heavier whereas those of *T. comptus* were more subdued.

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Taxonomic Review of the Australian *Drosophila setifemur* Species Group, a New Name for the *D. dispar* Species Group (Diptera: Drosophilidae)

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ABSTRACT. Examination of the holotype and a paratype of *Drosophila setifemur* Malloch, 1924 in the Australian Museum has resulted in the discovery that it is not a synonym of *D. sulfurigaster* as had previously been assumed. Instead, *D. setifemur* is a senior synonym of the widespread eastern Australian species *D. dispar* Mather, 1955. The so-called *Drosophila dispar* species group is renamed the *Drosophila setifemur* species group and *Drosophila unguicula* is removed from it. An illustrated key to Australian drosophilids with spinescent fore-femora is provided.

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The genus *Drosophila* accommodates a great range of drosophilids, with numerous aggregations at various levels between genus and species (viz. subgenus, species group, subgroup, complex, etc.). A rapidly growing body of knowledge is allowing us to know with ever increasing certainty the true genetic relationship between species. But ultimately, even when the tree that relates every lab strain and every field-sampled specimen is known with a high level of confidence, there will remain the task of affixing the taxonomically valid names to each of those samples and to biological species.

Drosophila currently has c. 1,600 described species; c. 350 are classified with *D. melanogaster* in the subgenus *Sophophora*, and another c. 730 species are treated as *Drosophila* s.str. Nearly all are attracted to fruit baits and can be established as cultures in the laboratory. The following synonymy involves *Drosophila dispar* Mather, 1955: 570 (a species in the *dispar* species group of the *Drosophila* subgenus *Sophophora*) and *D. setifemur* Malloch, 1924: 351 (a species incorrectly classified as synonymous with *D. sulfurigaster* (Duda, 1923: 48) in the *nasuta* subgroup, *immigrans* species group of *Drosophila* s.str.).

Removing *D. setifemur* from synonymy with *D. sulfurigaster* and placing it in synonymy with *D. dispar* leads to a need to rename the *Drosophila dispar* species group (established by Mather,1955).

Historical overview

When Malloch examined four specimens collected in Sydney, he found they were members of a new species which he named *Drosophila setifemur*—a fly with distinctive setation on both the posterior and anterior faces of the fore-femur. They were all females and the importance of this will become apparent below because there is marked sexual dimorphism in this species. In 1942, Patterson & Wheeler described *D. spinofemora* from a live culture originating from Honolulu, they used *spinofemora* as a name to denote distinctive but very short femoral spines. Yet another species, the widespread, peridomestic species *D. immigrans* Sturtevant, 1921: 83 also has a distinctive series of closely spaced femoral spines—seriate spinescent setulae. Patterson & Wheeler (1949) placed *D. spinofemora*, together with *D. setifemur* and 16 other species, in the *immigrans* species

group of *Drosophila* s.str. There is no indication in these studies that Patterson & Wheeler (1942, 1949) examined the *D. setifemur* holotype or paratype held in Sydney or either of the two paratypes held in the USNM (Lee *et al.*, 1956) before they included it in the *immigrans* species group.

Species of the *immigrans* group are collected at fruit and breed easily under culture making them ideal for genetic studies. The University of Melbourne geneticist, A.M. Clark, reported that between Malloch's 1924 publication and 1951 no further reports or collections of *D. setifemur* "seem to have been made" (Clark, 1957). If Clark was guided by the classification of Patterson & Wheeler (1949), and there is no reason to suspect otherwise, he would have been looking for a species differing only slightly from the cosmopolitan species *D. immigrans*; no such species exists in southeastern Australia (a region where the major cities are Melbourne, Sydney and Brisbane). In northern Australia, however, several species of the *immigrans* species group are abundant. Clark wrote (1957) that, in July 1951, he was able to obtain a few individuals of "*D. setifemur*" from *Drosophila* collections made with fermenting banana bait in the vicinity of Cairns, northern Queensland. His determination of these tropical Australian flies as *D. setifemur* was a mistake. The flies were most probably *D. sulfurigaster*, a fruit-breeding species now known to be very common in Cairns but a species then not reported from Australia. (It is important to note that, in 1957, very little had been published about Drosophilidae from tropical Australia.) The consequences of Clark's mis-identification were further compounded by his decision to re-describe *D. setifemur* based on these newly collected specimens (Clark, 1957). With hindsight it is not surprising that Clark's redescription of *D. setifemur* closely matches *D. sulfurigaster* not *D. setifemur* s.str. Clark nominated no voucher specimens and appears not to have examined the *D. setifemur* type in Sydney. It is also apparent that he had not noticed a list, published by Mather just several years earlier in 1955, of species collected in northern Queensland; the list included *D. spinofemora* (= *D. sulfurigaster*) from sites near Cairns, not *D. setifemur* s.str.

Clark (1957) found that the strain he determined to be *D. setifemur* (but which was probably *D. sulfurigaster*), hybridized freely with *D. spinofemora* (later shown to be a synonym of *sulfurigaster*), and so he considered it a useful model for comparative genetics. Twelve years later, in a wide-ranging study, the two were both placed in synonymy (Wilson *et al.,* 1969) with a third species *D. sulfurigaster* (type locality Madang, Papua New Guinea), which is widely distributed throughout the Pacific, tropical Australasian and Oriental Regions. Once again the holotype of *D. setifemur* appears not to have been examined. Rather, it seems likely that Wilson *et al.* (1969) relied too heavily on Clark's redescription and hybridization experiments which incorrectly concluded that "*D. setifemur*" was a species morphologically indistinguishable from *D. sulfurigaster* and one that hybridized freely with it. Wilson *et al.* (1969) may also have accepted, at face value, Mather's line of argument. In reference to the northern Queensland records of "*D. setifemur*" (see Clark, 1957) and "*D. spinofemora*" (see Mather 1953, 1955), Mather (1960: 237) wrote: "In view of the fact that *D. setifemur* and *D. spinofemora* have been shown to be sibling species (Clark, 1957) and *D. setifemur* is here shown to be abundant in northern Queensland, it seems likely that what was previously referred to as *D. spinofemora* was indeed *D. setifemur*". And finally, Wilson *et al.* (1969) may have been aware of, and influenced by, a then contemporaneous study by Mather, Baimai and Bock (1969) in which *D. setifemur* was incorrectly reported as common at fruit baits at five localities in Papua New Guinea.

The resulting confusion about the true identity of *D. setifemur* can be attributed firstly, to the false assumption that it had not, after 1924, been re-collected near Sydney; secondly, to its incorrect classification in the *immigrans* species group; thirdly, to its redescription based on specimens of *D. sulfurigaster*; fourthly, to incorrect records of its frequent occurrence at fruit bait in the Australasian tropics; and finally, to the fact that Malloch had described only females and had not reported the very distinctive sexual dimorphism in this species.

When Bock (Bock, 1976) undertook a major review of Australian *Drosophila* species he followed Wheeler (in Wilson *et al.*, 1969, see above) and accepted that *D. setifemur* was a junior synonym of *D. sulfurigaster*. However, he and other Australian *Drosophila* biologists—particularly Mather, Barker and Parsons—had accumulated extensive biogeographic data showing conclusively that *D. sulfurigaster* occurred neither in New South Wales (Bock & Parsons, 1978) nor in southern Queensland (Mather, 1955; but see van Klinken, 1996: 101). It therefore puzzled Bock (1976: 10) that Malloch had apparently described a common tropical species—one never found south of 20°S latitude—from four specimens collected in Sydney at 34°S. Had *D. sulfurigaster* once occurred in Sydney? Had there been an error in application of label-data? Or was *D. setifemur* not actually a synonym of *D. sulfurigaster*, was it a species known to be common in eastern temperate Australia under a different name?

Recent re-examination of certain type specimens in the Australian Museum, Sydney, curation of several hundred ex-SPHTM specimens accessioned in 1987 and assimilation of tens of thousands of eastern Australian field records (author's collections 1980 to present), has led to a re-assessment of *D. setifemur*. Among the ex-SPHTM material were additional specimens that had, around 1924, been classified, probably by Malloch or by F. H. Taylor, as being conspecific with *D. setifemur*. Such information, together with a better understanding of the biogeography and composition of the eastern Australian drosophilid fauna and examination of the *setifemur* holotype, has answered the questions posed above. *Drosophila setifemur* Malloch, 1924 is not a junior synonym of *D. sulfurigaster*, it is a senior synonym of *D. dispar* Mather, 1955.

Specimens referred to in this study are held in the following museums:

AMS	Australian Museum, Sydney.
ANIC	Australian National Insect Collection, CSIRO, Canberra.
BMNH	The Natural History Museum, London.
BPBM	Bernice P. Bishop Museum, Honolulu.
QM	Queensland Museum, Brisbane.
SPHTM	former School of Public Health and Tropical Medicine, University of Sydney, acalyptrate flies now incorporated in AMS.
USNM	United States National Museum (Smithsonian Institution), Washington.

Genus *Drosophila* Fallén, 1823

Subgenus *Sophophora* Sturtevant, 1939

Drosophila setifemur Malloch, 1924

Drosophila setifemur Malloch, 1924, *Proc. Linn. Soc. N.S.W.* 49: 351. Holotype ♀ and 1 paratype ♀ in AMS, 2 paratype ♀♀ in USNM; type locality Sydney, New South Wales, Australia.

Not *Drosophila setifemur* sensu Clark, 1957, *Aust. J. Zool.* 5: 216–222; Mather, Baimai & Bock, 1969: 72; Wilson *et al.*, 1969: 215–216.

Not *Drosophila sulfurigaster* (Duda, 1923) *Spinulophila*, *Annls hist.-nat. Mus. natn. hung.* 20: 48; Wilson *et al.*, 1969: 215–216.

Drosophila (Sophophora) dispar Mather, 1955, *Aust. J. Zool.* 3: 570 (and as redescribed by Bock, 1976: 19). Holotype ♂ in AMS, 24 paratypes, ex type culture, in AMS (including specimens once in SPHTM), ANIC, BMNH, QM, USNM; type locality Samford, near Brisbane, Queensland. **New synonym**.

Type material examined. ***Drosophila setifemur*** female holotype (AMS K50090, registered 20 September 1924) and one female paratype (also registered AMS K50090, but given a replacement number AMS K118452 in 2005) (two female paratypes in USNM [see Malloch, 1924; Lee *et al.*, 1956] not examined). ***Drosophila dispar***, holotype ♂, allotype, 4♂♂ and 4♀♀ paratypes (AMS K67819–K67824, K233649–K233652) (16 paratypes in the following museums [2♂♂ and 2♀♀ in each according to Mather, 1955: 547]: ANIC, USNM, QM, and BMNH not examined); all ex type culture, founded from one or several females collected at Samford, southern Queensland, 22 June 1953, W.B. Mather. These are holotypes and paratypes (see statement in preamble of Mather, 1955: 547) not syntypes as indicated by Daniels (Daniels, 1978: 440).

Other material examined. Numerous specimens of *Drosophila setifemur* (previously det. *D. dispar* by Mather, Bock, McEvey, Parsons, McAlpine), have been examined in the Australian Museum, the following is a list of 1923–2008 collecting localities arranged from lowest to highest latitude along Australia's east-coast, collectors include D. McAlpine, P. Parsons, C. Lambkin and S. McEvey: 12, Mt Bellenden Ker, 17.27°S (northern-most record); 2, Lake Eacham, 17.28°S; 3, The Crater NP, 17.42°S; 1, Laceys Creek, 17.85°S; 5, Paluma, 19.01°S; 1, Mt Dalrymple Rd, 21.13°S; 2, Mary Cairncross Park, 26.80°S; 1, Bunya Mountains, 26.85°S; 9, Mt Glorious, 27.33°S; 22, Samford, 27.37°S; 3, Joalah NP, 27.90°S; 1, Tamborine Mountain, 27.92°S; 3, Cunninghams Gap NP, 28.05°S; 120, Lamington NP, 28.14°S; 3, Binna Burra NP, 28.18°S; 1, Bilambil, 28.22°S; 3, Mt Warning NP, 28.40°S; 6, Toonumbar SF, 28.47°S; Tooloom Range, 28.48°S; Dome Mountain, 28.48°S; 1, Huonbrook, 28.53°S; 1, Whian Whian SF, 28.60°S; 8, Terania Creek, 28.67°S; Richmond Range, 28.81°S; Gibraltar Range, 29.47°S; Lowanna, 30.07°S; 1, Moonpar SF, 30.22°S; Bruxner Park, 30.24°S; 3, Dorrigo NP, 30.33°S; 1, Dingo Tops FP, 31.65°S; 1, Upper Allyn River, 32.13°S; Wootton, 32.31°S; 100+, Stroud garden, 32.41°S; 2, Mungo Brush, 32.53°S; 1, Palm Grove, 33.33°S; 4, Mount Wilson, 33.50°S; 1, Kurrajong, 33.55°S; 1, Mt Boyce, 33.62°S; 6, Springwood, 33.70°S; 3, Sydney, 33.88°S; 3, Palm Creek, 34.10°S; 5, Royal NP, 34.10°S; 1, Otford, 34.22°S; 2, Mt Keira, 34.40°S; 6, Mt Saddleback, 34.68°S; 3, Kangaroo Valley, 34.73°S; 1, Monga, 35.58°S; 10, Boyds Creek, 37.43°S; 1, Kinglake, 37.53°S; 1, Naghi SF, 37.55°S; 1, Hurstbridge, 37.63°S; 1, The Narrows, 37.88°S 147.97°E; 1, Ferntree Gully, 37.88°S 145.30°E (southern most Australian record, and western most Victorian record).

Redescription (based on *Drosophila setifemur*—McEvey Reg 25302, AMS K259065 male). Carina prominent but relatively narrow, ridged (ridge narrower in males, slightly broader in females). Thorax uniformly mid to dark brown. Male fore-femur plump with dense brush of erect hairs below; fore-metatarsus with a single, short, weak, curved, apical tooth; second tarsal segment with a similar tooth. Female fore-femur lacking dense brush and not unusually swollen; fore-tarsi without apical teeth. Abdomen glossy, blackish-brown, pale basally becoming black apically.

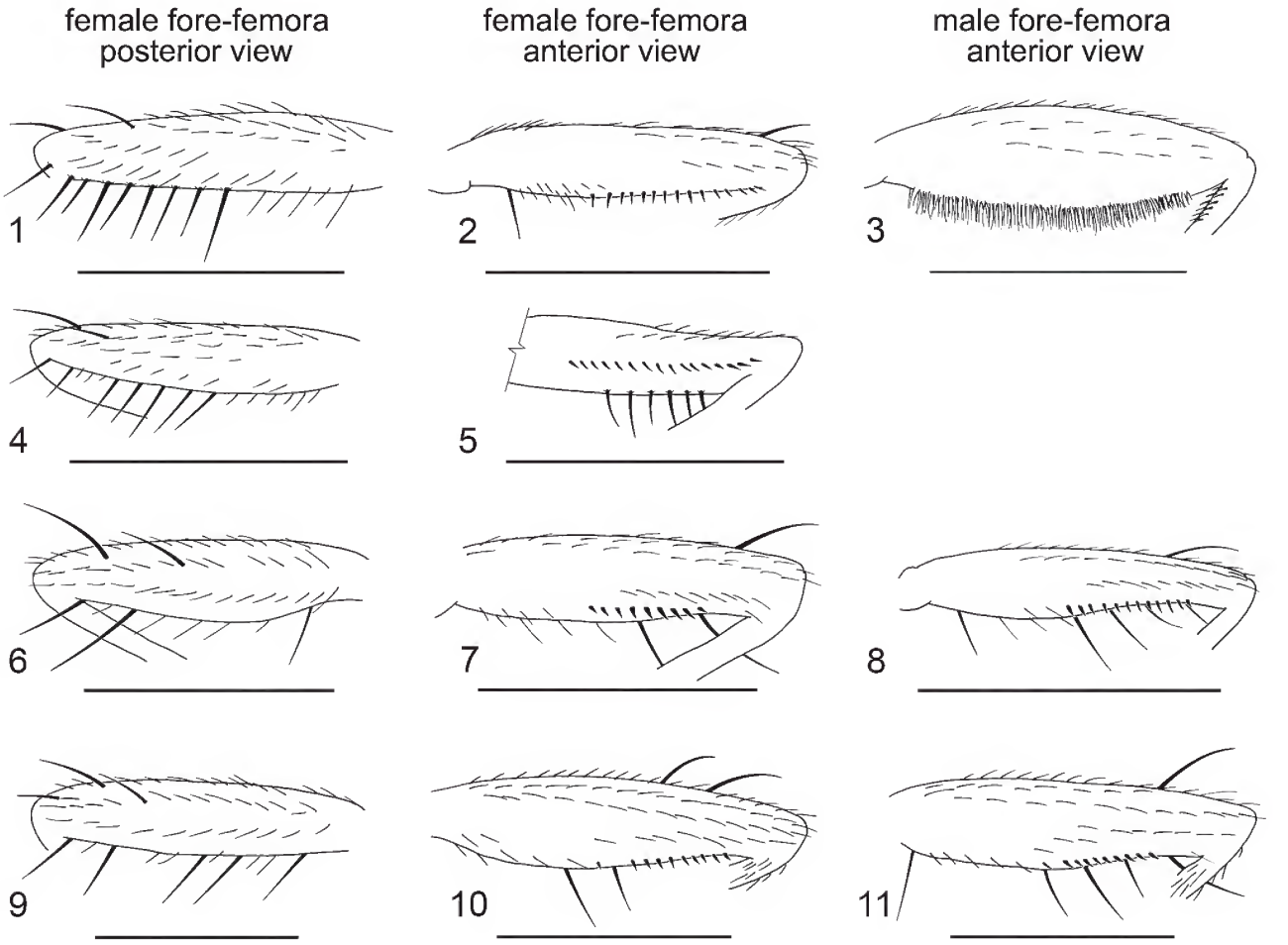
Body length. c. 2.5 mm.

Head. Arista with 4–5 branches above and 3 below plus terminal fork. Front very slightly broader than long, shining yellowish-brown; third antennal segment brownish; periorbital bands enclosing orbital and vertical bristles darker; ocellar triangle darker. Facial carina sharp and high, not broadened nor flattened below, lowest between antennal segments, highest and slightly pointed, in middle of face. Lower part of face distinctly darker than gena. Gena linear, pale; greatest width 0.1 greatest diameter of eye. Vibrissae duplicated, second about 0.9 of first. Eyes with dense fine pile. Orbital bristles in ratio 4: 1: 4; anterior reclinate fine, about equidistant between the proclinate and posterior reclinate, and slightly lateral to proclinate.

Thorax. Uniformly mid to dark brown, not vittate; lower part of postpronotum slightly paler. Acrostichal hairs in 8 irregular rows in front of dorsocentral bristles, 4–6 rows between dorsocentrals. Ratio anterior to posterior dorsocentrals 0.6. Prescutellars absent. Sterno-index 0.5–0.6. Legs pale yellowish-brown. Sex-comb of male consists only of 2 weak and slightly curved teeth, 1 apically on metatarsus, the second apically on 2nd tarsal segment (Bock, 1976: 19); because these teeth are so weakly developed, Mather (1955) is perhaps justified in describing this condition as "no sex comb". Both Bock (1976: 19) and Mather (1955: 571) refer to preapical bristles being on all tibiae; and apicals only on the mid-tibia, but I can find no clearly differentiated preapical setae on the fore tibiae in any of the males examined in this study.

Male fore-femur: plump, with numerous, fine, erect setulae brush-like on entire lower surface (Fig. 3); anteroventrally with no seriate spinescent setulae (cf. *sulfurigaster* males and females, compare Fig. 3 and Figs. 8, 11).

Female fore-femur: posteroventrally with a row of setae in slightly more than apical half (Figs. 1 and 4), all setae subequal in length, evenly spaced and shorter than or equal to the femoral diameter. In describing the holotype female Malloch wrote (1924: 351), and it is here confirmed, that the "fore-femur [is] with short closely placed fine setulae on more than the apical half of posteroventral surface, the



Figures 1–11. Fore-femora of *Drosophila setifemur, D. sulfurigaster* and *D. immigrans* showing sexual dimorphism in *D. setifemur* and setation on anteroventral and posteroventral surfaces. (1–5) *Drosophila setifemur*: (*1*), *D. dispar* Mather (= *D. setifemur* Malloch) allotype female, Samford, Queensland, AMS K67820; (*2*), *D. dispar* Mather paratype female, Samford, Queensland, AMS K67825; (*3*), *D. dispar* holotype male, Samford, Queensland, AMS K67819; (*4*) and (*5*) (the latter is a ventral view showing both anterior and posterior setation of fore-femur), *D. setifemur* female paratype, Sydney, AMS K50090. (6–8) *Drosophila sulfurigaster*: (*6*) and (*7*), female, Malololelei, Samoa, McE 21321; (*8*), male, AMS K 234064, Maple Creek, near Innisfail, Queensland. (9–11) *Drosophila immigrans*: (*9*) and (*10*), female, near Ebor, New South Wales, AMS K234065; (*11*), male, Sydney, AMS K234066. Scale 0.5 mm.

longest one, at apex, not longer than the femoral diameter". This is *not* a reference to the seriate spinescent setulae on the anteroventral surface. Female fore-femur not swollen, without brush of erect setulae below as in males (compare Fig. 2 and 3); anteroventrally with seriate spinescent setulae (Figs. 2 and 5).

Abdomen glossy, blackish-brown, paler basally, becoming black apically. Halteres yellow.

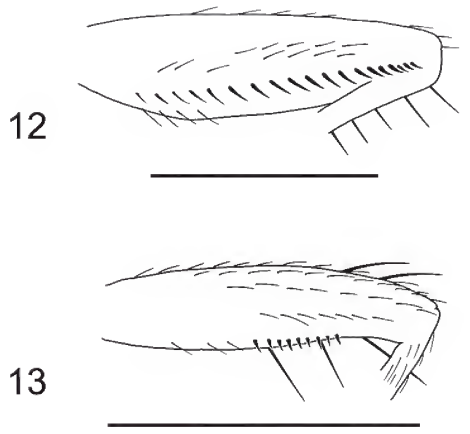
Wings (*D. setifemur* holotype AMS K50090). Hyaline. *C*-index = 2.38; *4v*-index = 2.04; *5x*-index = 1.76; *4c*-index = 1.12; *ac*-index 2.57; *M*-index = 0.61; third costal section with fringe of heavy setation on basal 0.67. Length, from humeral crossvein to apex, 2.2 mm (from axis to apex, c. 2.5 mm).

Male terminalia. Cercus very small with very long finger-like process extending from below (Mather, 1955, fig. 11C; Bock, 1976, fig. 9); the latter is translucent (not heavily sclerotized), strongly curved, tapering to a point, and protrudes well outside the body making it, and the opposing one, clearly visible under low magnification. Under high magnification several sensilla are visible on these processes subapically. Aedeagus with prominent subapical ornamentation.

Distribution. Type locality is Sydney, Australia where the species is taken frequently at fruit baits in urban bushland (Table 1). This species has been collected at numerous sites in eastern Australia (see above) from northern Queensland at the summit of Mt Bellenden Ker (1561 m) to Ferntree Gully, outer eastern suburb of Melbourne, Victoria. It apparently does not overlap with the range of *D. prodispar* Parsons & Bock, 1982, in western Victoria.

Notes

Drosophila setifemur closely resembles *D. prodispar* and is therefore probably closely related to it. The structure of the male and female terminalia, the sexually dimorphic fore-femur and the generally dark coloration of these flies make them quite unlike others in the *Drosophila* subgenus *Sophophora*.



Figures 12–13. Anteroventral setation of fore-femora of *Drosophila teratos* and *D. niveifrons*. (*12*) *Drosophila teratos*, male, Lake Eacham, Queensland, AMS K233710. (*13*) *Drosophila niveifrons*, male, Wanigela, Papua New Guinea, AMS 234063. Scale 0.5 mm (a *niveifrons* paratype [marked ex stock 14.x.1979 Kitagawa *et al.*] in BPBM has 8–9 spinescent setulae, McEvey pers. obs. 26.xi.2008).

A variety of different terms have been applied to the spinescent setulae lying in a series along the lower anterior surface of the fore-femur, and there has been a tendency to emphasize only this aspect of the femoral setation, ignoring the taxonomically useful arrangement of long setae on the posteroventral surface. Reference is made, for example, to "short, stout, spine-like bristles on lower apical part of fore femora" (Patterson & Wheeler, 1942); "comb-like series of stout bristles on femur" (Mather, 1955); "row of … short, stout, microscopic setae on the apical half of the anteroventral surface of the fore femur" (Clark, 1957); "fore femur with more or less well developed row of short stout comb-like teeth (femoral comb)" (Bock, 1976); "the comb-like bristle row on the inner side of the first femur" (Wilson *et al.,* 1969). It is only Malloch (1924) however, who made reference to the diagnostic utility of the setation on the posterior side of the fore-femur. Indeed it is the relative length and arrangement of long setae arising from the lower fore-femur on its posterior side that offers a more definitive means of separating species of the *immigrans* and *setifemur* species groups, at least in females. Males of *D. setifemur* completely lack serial spinescent setulae and have instead a thick brush of erect hairs (Fig. 3).

When comparing *Drosophila prodispar* and *D. setifemur,* Parsons & Bock wrote that both "species show the same dimorphism in carina width and hypertrophy of the fore-femur. However, examination of the genitalia under the higher powers of a stereo microscope reveals diagnostic differences in both sexes. In the male, the aedeagus is cylindrical in *dispar* [= *setifemur*] but broadly flattened in *prodispar*; a long slender curved finger-like process extending from the genital arch [sic] is visible on each side in *dispar* [= *setifemur*], while the corresponding process in *prodispar* is shorter, wider and barely curved. In the female, the egg guide in *dispar* [= *setifemur*] possesses a slender apical extension bearing fine teeth; in *prodispar* the egg guide possesses no apical extension and fine teeth are absent. These differences are evident in pinned specimens and should also be obvious in live flies" (Parsons & Bock in Bock, 1982: 53). As specimens of *D. setifemur* and *D. prodispar* examined by me in the AM have a distinctive extension of the cercus, not the genital arch, I believe the above reference to an extension of the "genital arch" (epandrium) is an error. Note also that sexual dimorphism in the width of the carina is rather subtle.

The *Drosophila setifemur* species group

Within the Drosophilidae, but not generally in the Diptera, there is an informal and hierarchical classification between the genus level and the species level. For example, the *melanogaster* "species group" accommodates a large number of species that share morphological characteristics with *D. melanogaster* (Bock & Wheeler, 1972; Bock, 1980) and are phylogenetically closely related (Lemeunier *et al.,* 1986). The "species group" is a superspecific aggregation with a rank below subgenus, it is divided into various "subgroups", subgroups are sometimes divided into "complexes", and complexes into sibling pairs, cryptic species or other loosely defined groupings of small numbers of species. (Subspecies is a rank seldom used in the Drosophilidae.) Guidelines for the application of these subgeneric and superspecific names are not offered by the ICZN and so it is difficult to affect an objective re-appraisal of the so-called "*dispar* species group", now that the correct name of the typical species is no longer *D. dispar*. There is also the untidy situation of synonymy with the "*dispar* species group" in another drosophilid genus *Zygothrica*; this clash would be rectified if the *Drosophila dispar* species group was renamed.

The logical course of action, and the one adopted here, is to replace the name "*Drosophila dispar* species group" with the name "*Drosophila setifemur* species group". This is done in anticipation of confusion that might result were nothing done. In light of the current systematic uncertainties due to the polyphyletic assemblage of species in *Drosophila* (O'Grady & DeSalle, 2008) it would be premature to consider erecting a new genus or new subgenus to accommodate *D. setifemur* and *D. prodispar* although the atypical male terminalia (especially the acuminate extension of the lower cercus and the form of the ventral projections of the epandrium are quite unlike any other in the *Drosophila* subgenus *Sophophora*) offers a suitable starting point for such a consideration. The typical species of the species group is *D. setifemur*, and *D. prodispar* is the only other member. Prior to the present investigation, however, it was generally accepted that the "*Drosophila dispar* species group" had three species (e.g., Ashburner *et al*., 2005) viz. *D. dispar* [= *setifemur*], *D. prodispar* and *D. unguicula* Okada & Carson, 1983:138. Okada & Carson (1983) speculated that *D. unguicula* from Papua New Guinea "seems to belong to the *dispar* [=*setifemur*] species group" but the "cercus [is] with a strong black spur ventrally" and in this respect it is quite unlike *D. setifemur* which has instead a long acuminate process with subapical trichose hairs. *Drosophila unguicula* has not been examined in this study but in light of the description and illustrations offered by Okada and Carson and the detailed examination of the *D. setifemur* and *D. prodispar* genitalia in the present study, it is concluded that *D. unguicula* should be excluded from the *setifemur* species group.

Other species examined. ***Drosophila prodispar*** Parsons & Bock, in Bock, 1982: 51, four paratypes as follows: 1, Paradise, Otway Rd., Vic., off fronds, 20.v.1975, P.A. Parsons, AMS K72928; 1, Paradise, Otway Rd, Victoria off tree ferns, 21.v.1975, P.A. Parsons, AMS K72929; 2, River on Horden Vale Rd., Otway Rd., Vic., dampish habitat, off sedge 12.ix.1975, P.A. Parsons, AMS K232905 and AMS K232906. ***Drosophila teratos*** Bock, 1982: 89.—holotype, [Royal] National Park N.S.W. 3.11.1956, D.K. McAlpine, AMS K73142; Lake Eacham NP Qld, swept off fungi, June 1983, P.A. Parsons, AMS K233710 (det Bock, 1983) fore-femur figured (Fig. 12); QLD: 28.212°S 153.141°E, Lamington NP IBISCA Qld, Plot# IQ-500-B 514 m, 21–26 Jul. 2007, rainforest, Lambkin, Starick, Monteith, Malaise trap 23186, QM T155510 (det McEvey, 2008). ***Drosophila sulfurigaster*** (Duda).—numerous specimens examined in the AMS from islands of the Pacific Ocean: Papua New Guinea, New Ireland, Fiji, Samoa, New Caledonia, Loyalty Islands, Vanuatu, Solomon Islands, Marquesas, Moorea and Tahiti; specimens in the AMS from the Oriental Region: Vietnam, Malaysia, Borneo, Luzon, Guam and Christmas Island (Indian Ocean); and specimens in the AMS from Australia (see Figs. 6–8): Moa I. (10.2°S), Thursday I., Mt Adolphus I., Heathlands (11.7°S), Iron Range, Claudie Rv., Gordon Ck (12.7°S), Cooktown (15°S), Cape Tribulation (16.2°S), Mossman Gorge, Kuranda, Cairns (16.9°S), Mulgrave Rv. (17.2°S), Palmerston NP, Maple Ck (17.6°S), Paluma (19°S), Townsville (19.3°S), Campaspe Rv (20.4°S). ***Drosophila (Drosophila) niveifrons*** Okada & Carson, 1982: 407.—1♂, PNG, Wanigela, 9°16'S 149°08'E, 12–28 Feb 2003, S.F. McEvey, McE 20105, AMS 234063; fore-femur figured (Fig. 13). ***Drosophila (Drosophila) immigrans*** Sturtevant.—1♀, NSW Pinegrove HS, 13km SW Ebor, 1130m, 30°29.935'S 152°16.014'E, banana 17–18 January 2000, Barker McEvey Polak Starmer, McE 14225, AMS 234065; fore-femur figured (Figs. 9–11).

A key to Australian species of *Drosophila* with seriate spinescent setulae on fore-femur

Seven *Drosophila* species that occur in temperate and tropical forests of eastern and northeastern Australia and New Guinea could be confused with *Drosophila setifemur* because, except for males of *D. setifemur*, they all have seriate spinescent setulae anteroventrally on the fore-femur—the following key allows them to be correctly identified.

1 Vibrissa single ..... *Drosophila teratos*

—— Vibrissa double 2

2 Males 3

—— Females 8

3 Fore femur distinctly swollen (often collapsed and flattened in pinned specimens), densely hirsute ventrally along its entire length, and without distinctive series of spinescent setulae in apical, anteroventral, half (Fig. 3); terminalia characterized by a pair of long, slender, semi-translucent, appendages usually visible without dissection 4

—— Fore femur not distinctly swollen, rarely collapsed in pinned specimens, diameter of fore-, mid-, and hind-femora subequal, ventral surface with a few scattered hairs near base only, with distinctive series of short spines in apical, anteroventral, half (Figs. 8, 11–13); many setae on posteroventral surface of fore-femur longer than femoral diameter; terminalia without slender appendages as described above 5

4 Appendages of terminalia tapering to a point apically and strongly curved, Eastern Australia ..... *Drosophila setifemur*

—— Appendages of terminalia blunt apically and not strongly curved, western Victoria ..... *Drosophila prodispar*

5 Thorax and abdomen blackened ventrally; weakly developed seriate spinescent setulae on fore-femur ..... *Drosophila rubida* Mather, 1960

—— Thorax and abdomen not blackened ventrally; strongly developed seriate spinescent setulae on fore-femur 6

6 Abdominal tergites with broad apical black bands dorsally only, fringe of heavy setation in about 0.3–0.4 of third costal section (common at fruit baits and compost in cool temperate Australia, peridomestic worldwide distribution), front without distinctive silvery pruinescence ..... *Drosophila immigrans*

—— Abdomen largely pale, stramineous (straw yellow), fringe of heavy setation in about 0.5–0.7 of third costal section (tropical northeastern Australia, north of 20°S latitude), front with distinctive pruinescence in males only 7

7 Male fronto-orbits only, with distinct silvery pruinescence, visible especially at acute angles ..... *Drosophila sulfurigaster*

—— Male frons entirely covered with distinct silvery pruinescence, visible especially at acute angles ..... *Drosophila niveifrons*

8 Female fore-femur with short closely spaced setae on more than the apical half of posteroventral surface, the longest one, at apex, not longer than the femoral diameter (Figs. 1, 4); C-index about 2.4 (third costal section not less than a third the length of the second section); facial carina narrow; thorax brown, abdomen blackish-brown, subshining ..... *Drosophila setifemur* and *D. prodispar*

—— Female fore-femur with four or five widely spaced bristles on the entire length of posteroventral surface, the longest one, at or near middle, as long as or longer than the femoral diameter (Figs. 6, 9); C-index 3.7–4.7, facial carina very broad ..... *Drosophila immigrans, D. rubida, D. sulfurigaster, D. niveifrons*

Biogeography and habitat preference

A comprehensive morphological and genetic study of *Drosophila setifemur* and *D. prodispar*, especially where their ranges meet (or almost meet) near Melbourne, Victoria, could lead to a convenient new model for studying environmental adaptation, speciation and interspecific hybridization (note that *setifemur* × *prodispar* hybridization is currently unknown). *Drosophila prodispar* appears to occur only in the *Otway Natural Region* (Barlow, 1985) west of Melbourne while *D. setifemur* occurs in eastern Australia from just east of Melbourne to Queensland (*Howe, Nepean, McPherson* to *Cape York Natural Regions*).

Extensive fruit-baiting in Tasmania and the islands of Bass Strait might result in the discovery of additional isolated populations or even other species, although there is no evidence that any drosophilid speciation has resulted from sea-level rise in Bass Strait (Parsons & Bock, 1977).

Atkinson (1985) has recorded *D. setifemur* (as *D. dispar*) on Black Apple *Planchonella australis* at Bruxner Park (30.2°S 153.1°E) near Coffs Harbour but numerous other fruits, flowers and fungi appear to be suitable for breeding. Moxon *et al.* (1982) report it as common at fruit and mushroom baits "from north Queensland–Victoria especially in floristically depauperate forests." My collection records also indicate that it is common in fern and bracken (*Pteridium*) habitats, and is attracted to composted and rotting vegetables, flowers of *Syzygium,* rotting fruits of, for example, *Citrus, Feijoa,* and *Opuntia,* rotting mushrooms and other fungus, and it is taken in Malaise and pitfall traps. Parsons & Bock (1977) also note that *D. setifemur* (as "*D. dispar*") is attracted to both mushroom and fermented fruit baits throughout its range, particularly in tree fern, *Eucalyptus–Acacia* and sedge habitats, but interestingly, to the west of Melbourne, they collected flies (which, by inference, must have been *D. prodispar*) only by sweeping and not at all by fruit- or mushroom-baiting. This suggests that it may be difficult to establish *D. prodispar* in culture.

Collection records for drosophilid flies collected at fruit bait in the *Nepean Natural Region* (which includes Sydney, Barlow, 1985), indicate that *Drosophila setifemur* is the most common species when using this method in natural or semi-natural habitats (Table 1).

Table 1. The most frequently collected species of Drosophilidae using fruit baits in semi-natural habitats in the Sydney region with approximate abundance ratio indicated as a percentage (pooled data, variation between traps can be large).

Drosophila setifemur Malloch, 1924	29%
Drosophila immigrans Sturtevant, 1921	19%
Drosophila simulans Sturtevant, 1919	17%
Scaptodrosophila lativittata (Malloch, 1923)	11%
Drosophila pseudotakahashii Mather, 1957	9%
Drosophila serrata Malloch, 1927	6%
Drosophila melanogaster Meigen, 1830	3%
Scaptodrosophila sydneyensis (Malloch, 1927)	3%
Scaptodrosophila claytoni van Klinken, 1997	2%
Scaptomyza australis Malloch, 1923	1%

ACKNOWLEDGMENTS. Preparation of the Australian Drosophilidae Checklist supported by Australian Biological Resources Survey (ABRS) led to the discovery of synonymy of *dispar* and *setifemur*. Extensive collecting in the Sydney region for the Australian Museum Pilot GIS Survey in 1991 was supported by an Australian Museum Visiting Scientist Research Fellowship for which I am most grateful. Many other records of the species discussed here are the result of drosophilid surveys supported by the Northeast New South Wales Forests Survey (NSW NPWS); and the IBISCA surveys of Lamington NP. Other specimens examined in this study were collected by P. Parsons, R. van Klinken, J.S.F. Barker, D. McAlpine, M. Polak, W. Starmer, M. Schiffer, D. Britton, C. Lambkin, N. Starick, and D. Wright. I thank David McAlpine, Dan Bickel, Gerhard Bächli and Michele Schiffer for useful comments.

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New Records of Plio-Pleistocene Koalas from Australia: Palaeoecological and Taxonomic Implications

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ABSTRACT. Koalas (Phascolarctidae, Marsupialia) are generally rare components of the Australian fossil record. However, new specimens of fossil koalas were recovered during recent systematic excavations from several eastern Plio-Pleistocene deposits of Queensland, eastern Australia, including the regions of Chinchilla, Marmor and Mt. Etna. The new records are significant in that they extend the temporal and geographic range of Plio-Pleistocene koalas from southern and southeastern Australia, to northeastern central Queensland. We provide the first unambiguous evidence of koalas in the Pliocene Chinchilla Local Fauna (phascolarctid indet. and *Ph. ?stirtoni*): important additions to an increasingly diverse arboreal mammalian assemblage that also includes tree kangaroos. The persistence of koalas and local extinction of tree kangaroos in the Chinchilla region today suggests that significant habitat and faunal reorganization occurred between the Pliocene and Recent, presumably reflecting the expansion of open woodlands and grasslands. Other koala records from the newly U/Th-dated Middle Pleistocene Marmor and Mt. Etna fossil deposits (*Phascolarctos* sp. and *Ph. ?stirtoni*), along with independent palaeohabitat proxies, indicate the former presence of heterogeneous habitats comprised of rainforests, open woodlands and grasslands. The lack of such habitat mosaics in those regions today is likely the product of significant Middle Pleistocene climate change.

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Koalas (Phascolarctidae, Marsupialia) are Australian endemic, relatively large-sized (c. 10 kg), arboreal marsupials that occupy a similar ecological niche to placental lemuroids or sloths (Murray, 1984). The modern Koala, *Phascolarctos cinereus*, is the only surviving member of an ancient and diverse family of marsupials, with the oldest members known from the Late Oligocene (Black, 1999). Six to seven genera and 18 species (several undescribed) are currently recognized (Black, 1999). Phascolarctids are separated from all other vombatiformes (i.e., wombats, marsupial "lions", illarids, wynyardiids, maradids, and diprotodontoids) on the basis of their selenodont dental morphology and occupy a position near the base of the diprotodontian ordinal tree (Archer, 1976; Archer & Hand, 1987). A recent molecular phylogeny supermatrix, temporally-constrained using dated occurrences of fossil taxa, suggested that koalas diverged from vombatoids during the Middle Eocene (Beck, 2008).

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Koalas are generally rare components of the Australian fossil record, presumably reflecting their arboreal habits (Murray, 1991), and fossil koala material is commonly fragmentary and/or poorly preserved. Thus, determination of intra- and interfamilial phascolarctid relationships has proven difficult. Pre-Holocene koalas are known from Oligo-Miocene deposits of Riversleigh, Frome Basin, and Tirari Desert (Stirton *et al.*, 1967; Woodburne *et al.*, 1987; Black & Archer, 1997; Myers *et al.*, 2001; Louys *et al.*, 2007); Late Miocene-Pliocene deposits of Corra Lynn Cave and Waikerie (Pledge, 1987); and Pleistocene deposits of Koala Cave, Mammoth Cave, Devil's Lair, Tight Entrance Cave, Lake Eyre region, Madura Cave, Lake Menindee, Lake Victoria, Nelson Bay, Naracoorte region, Wellington Caves, and Gore (Bartholomai, 1968; Merrilees, 1968; Archer, 1972; Balme *et al.*, 1978; Lundelius & Turnbull, 1982; Tedford & Wells, 1990; Archer *et al.*, 1997; Dawson & Augee, 1997; Moriarty *et al.*, 2000; Reed & Bourne, 2000; Piper, 2005; Ayliffe *et al.*, 2008; Price, 2008a) (Fig. 1). The koala fossil record from the central to north eastern margin of the Australian continent is particularly depauperate, with only one specimen known (type specimen of *Phascolarctos stirtoni* from Gore, southeast Queensland). *Koobor*, a koala-like vombatiform marsupial is also known from isolated specimens from the Bluff Downs (central eastern Queensland) and Chinchilla Local Faunas (southeastern Queensland (Archer & Wade, 1976; Archer, 1977a). Although originally considered to be a koala, more recent morphology-based phylogenic analyses suggest that *Koobor* sits outside the Phascolarctidae (Black & Archer, 1997) and may actually be a primitive sister-group of wynyardiids and ilariids (Myers & Archer, 1997).

Here we report new specimens of fossil koalas that were recovered during recent systematic excavations from several Plio-Pleistocene deposits of eastern Queensland, including the regions of Chinchilla, Marmor and Mt. Etna (Fig. 1). Although the new specimens are fragmentary, the paucity of information about koalas in the Plio-Pleistocene makes the new eastern Australian material particularly noteworthy. Thus, the aim of this paper is to describe the new material and discuss the taxonomic and palaeoecological implications within a reliable geochronological framework.

Materials and methods

Dating. Samples of bone and post-depositional calcite growth within long-bone hollows from the Marmor and Mt. Etna cave fossil deposits were targeted for thermal ionization mass spectrometry (TIMS) U/Th dating. Each sample was pre-treated and processed at the Radiogenic Isotope Facility, The University of Queensland, following techniques described in Zhao *et al.* (2001) and Yu *et al.* (2006).

Speleothem calcites and aragonites are secondary mineral deposits that form in cave environments. Uranium is commonly leached from downward percolating meteoric waters and becomes co-precipitated within speleothem calcite (or aragonite) during genesis. At the time of speleothem formation, some U, but little or no Th, is incorporated into the calcite (or aragonite) lattices, and disequilibrium in the U-series decay chain occurs. The U/Th age is calculated by determining the amount of ^{230}Th that was produced by the decay of ^{238}U (via intermediate isotope ^{234}U). Thus, dating of speleothem material provides the true age of initial calcite crystallization. However, in this dating study, the calcite precipitated within long bone hollows at some stage after deposition, thus, the calculated U/Th ages will represent minimum ages for the associated faunal assemblages.

Fresh bone and teeth contains little or no U. However, after burial, U is taken up from the environment by bone apatites that scavenge U, but exclude Th, during diagenesis. Unlike speleothem, bones and teeth are open systems for U (Grün *et al.*, 2008), therefore, the U/Th dates commonly represent the mean age of U-uptake history. Thus, a calculated age most likely represents a minimum age for the dated bone or tooth. This has previously been demonstrated for eastern Australian cave deposits where U/Th dating of deposit-capping speleothem (thus, also representing minimum ages) return dates that are always older than U/Th dated bone and teeth recovered from within the deposit itself (Hocknull *et al.*, 2007).

Unfortunately, U/Th datable material that could potentially produce maximum ages of deposition was not recovered from the Marmor and Mt. Etna koala deposits. No dateable samples were obtained from the Chinchilla fossil deposits.

Terminology. Dental nomenclature follows Luckett (1993) where the adult unreduced cheek tooth formula of marsupials is P1–3 and M1–4 in both upper and lower dentitions. Dental cusp terminology follows Archer (1978) except for what was then interpreted to be the hypocone, is now regarded to be the metaconule, based on its linkage through the postprotocrista with the protocone and metacone (Tedford & Woodburne, 1987; Tedford & Woodburne, 1998). Higher-level systematic nomenclature follows Aplin & Archer (1987). All measurements were made using callipers and are given in millimetres (mm).

Institutional abbreviations. QMF, Queensland Museum Fossil specimen, Queensland Museum, Brisbane, Australia; QMJ, Queensland Museum modern specimen, Queensland Museum, Brisbane, Australia; QML, Queensland Museum fossil Locality, Queensland Museum, Brisbane, Australia; SAMP, South Australian Museum Palaeontological specimen, South Australian Museum, Adelaide, Australia.

Geographic and geological settings

Chinchilla. Site QML7 is located in Chinchilla, south-eastern Queensland (Fig. 1). Vertebrate fossils, constituting the Chinchilla Local Fauna, are predominantly derived from the Chinchilla Sand, a lithostratigraphic sequence of fluviatile sediments exposed in the Condamine River between Nangram Lagoon and Warra (Woods, 1960). The Chinchilla Sand includes well-lithified calcareous sandstones grading into siltstone and conglomerate (quartz and ferruginous sandstone), and weakly consolidated sands that grade into silt and sandy clay. Such sediments were derived from erosion of the Orallo Formation and its lateritized profiles (Bartholomai & Woods, 1976). There are no analytical dates associated with the Chinchilla Sand. However, biochronological correlation based on fossil vertebrates to other important radiometrically-dated faunas from elsewhere in Australia (e.g., Kanunka Local Fauna,

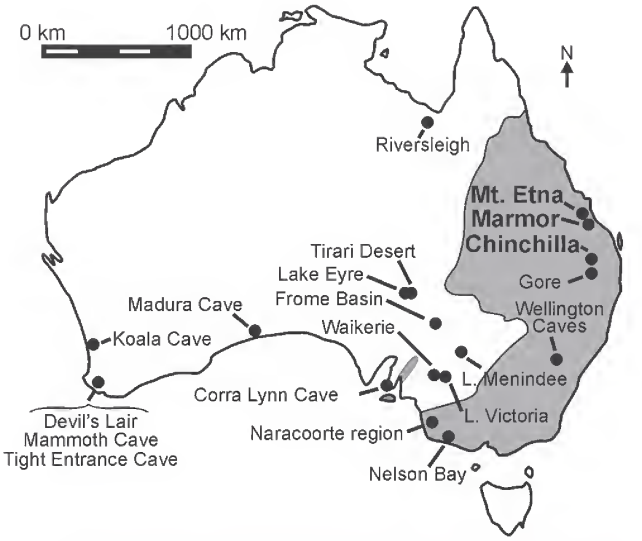

Fig. 1. Oligocene-Pleistocene fossil localities where koalas have been recovered, including present study sites (Chinchilla, Marmor and Mt. Etna). Shaded area indicates historic (i.e., post-European settlement in Australia) geographic range of the modern Koala, *Phascolarctos cinereus*.

Bluff Downs Local Fauna, and Hamilton Local Fauna), suggests a Middle Pliocene age (Whitelaw, 1991; Tedford *et al.*, 1992; Mackness *et al.*, 2000).

Marmor. Site QML1420 is located in Marmor, central eastern Queensland (Fig. 1). QML1420 is a brecciated limestone cave deposit, with sediments dominated by grey to brown clays and limestone clasts (Hocknull, 2005). The deposit contains typical Pleistocene megafauna including *Diprotodon optatum*, *Thylacoleo carnifex* and *Macropus giganteus titan* (Longman, 1925) (*D. optatum* and *M. g. titan* taxonomy up-dated following Price (2008b) and Dawson & Flannery (1985), respectively). Direct U/Th dating based on teeth from such taxa returned minimum ages of 122–154 ka (Table 1) suggesting that the assemblage is Middle Pleistocene or older. The assemblage lacks faunal elements typical of Pliocene assemblages and on the basis of biocorrelation to nearby well-dated deposits of the Mt. Etna region (Hocknull *et al.*, 2007), site QML1420 is unlikely to be older than Middle Pleistocene.

Mount Etna. Site QML1384 (Unit "L.U."; Elephant Hole Cave) is located at Mt. Etna, central eastern Queensland (Fig. 1). It is a brecciated limestone cave deposit, with sediments dominated by red/yellow/grey clays with occasional gravel and cobbles (Hocknull, 2005). Direct U/Th dating based on a macropod bone provided an age of 267±5.2 ka (Table 1). However, due to unknown rates of U uptake, the date should be regarded as a minimum age only. This interpretation is supported by U/Th dating of calcite recovered from the hollow of long bone, which returned an age of 331.6±14 ka (Table 1). This age is likely to be closer to, but still younger than, the true age of the fossil assemblage. A maximum age has not been determined for QML1384 "L.U.", but based on faunal similarities to other dated sequences in the region, the deposit is unlikely to be older than 500 ka (Hocknull *et al.*, 2007).

Systematic Palaeontology

Super cohort Marsupialia Cuvier, 1817

Order Diprotodontia Owen, 1866

Suborder Vombatiformes Woodburne, 1984

Infraorder Phascolarctomorphia Aplin & Archer, 1987

Family Phascolarctidae Owen, 1839

Phascolarctidae gen. et sp. indet.

Figs 2, 3A

Referred material. QMF52287, left dentary fragment, QML7, Chinchilla, southeast Queensland, Australia (Pliocene).

Description. Dentary fragment with horizontal ramus broken anterior to P_3 alveolus and posterior to M_3 alveolus; surface bone slightly root-etched; cheek teeth crowns missing, roots present, alveolar border broken buccally; ventral border slightly in-turned lingually; mental foramen anteroventral to P_3 anterior alveolus; posterior mental foramen well developed, ventral to position between posterior root of M_1 and anterior root of M_2; symphysis strongly fused, very deep, extended posteriorly to below posterior root of M_1, kinked such that posteroventral border extends below ventral border of horizontal ramus, inclined posteriorly at posteroventral margin, inclined anteriorly at a low angle (35°); genial pit, c. 3 mm largest diameter, present at posterior ventral portion of symphysis, similar symmetrical but broken pit present on opposing dentary.

Remarks. The dentary fragment is considered to be adult based on the presence of well-developed P_3 and M_3 alveoli, and a strongly fused symphysis. The dentary resembles phascolarctids in general morphology. However, QMF52287 does not appear to be referable to any phascolarctid where the dentary is known. It differs from *Nimiokoala*, *Perikoala*, *Madakoala*, and *Phascolarctos cinereus* by: (*a*) being significantly more robust in terms of depth and width (Fig. 3A); (*b*) possessing a more anteriorly positioned posterior mental foramen; (*c*) having a straighter ventral border; and (*d*) by possessing a relatively deeper symphysis that has a lower anterior ascending angle. QMF52287 is more gracile in comparison to *Cundokoala yorkensis* (a genus that is questionably distinct from *Phascolarctos*; see Black, 1999) (Fig. 3A), but like *Ph. cinereus*, also differs from the former taxon in having a more anteriorly positioned posterior mental foramen, straighter ventral border, and deeper symphysis. The dentary of *Litokoala* is unknown, but on the basis of alveoli dimensions, is probably significantly smaller than QMF52287. QMF52287 differs from *Perikoala* and *Madakoala* in that the symphysis is more strongly fused, and the diastema is relatively longer. Well-developed symmetrical genial pits are present at the posteroventral base of the symphysis of QMF52287, but are not expressed as strongly in other koala genera. Well-developed genial pits occur in wombats such as *Vombatus*, but such pits are relatively larger, positioned relatively higher from the ventral border, and the pits commonly converge on each other on the left and right side of the symphyseal fusion forming a

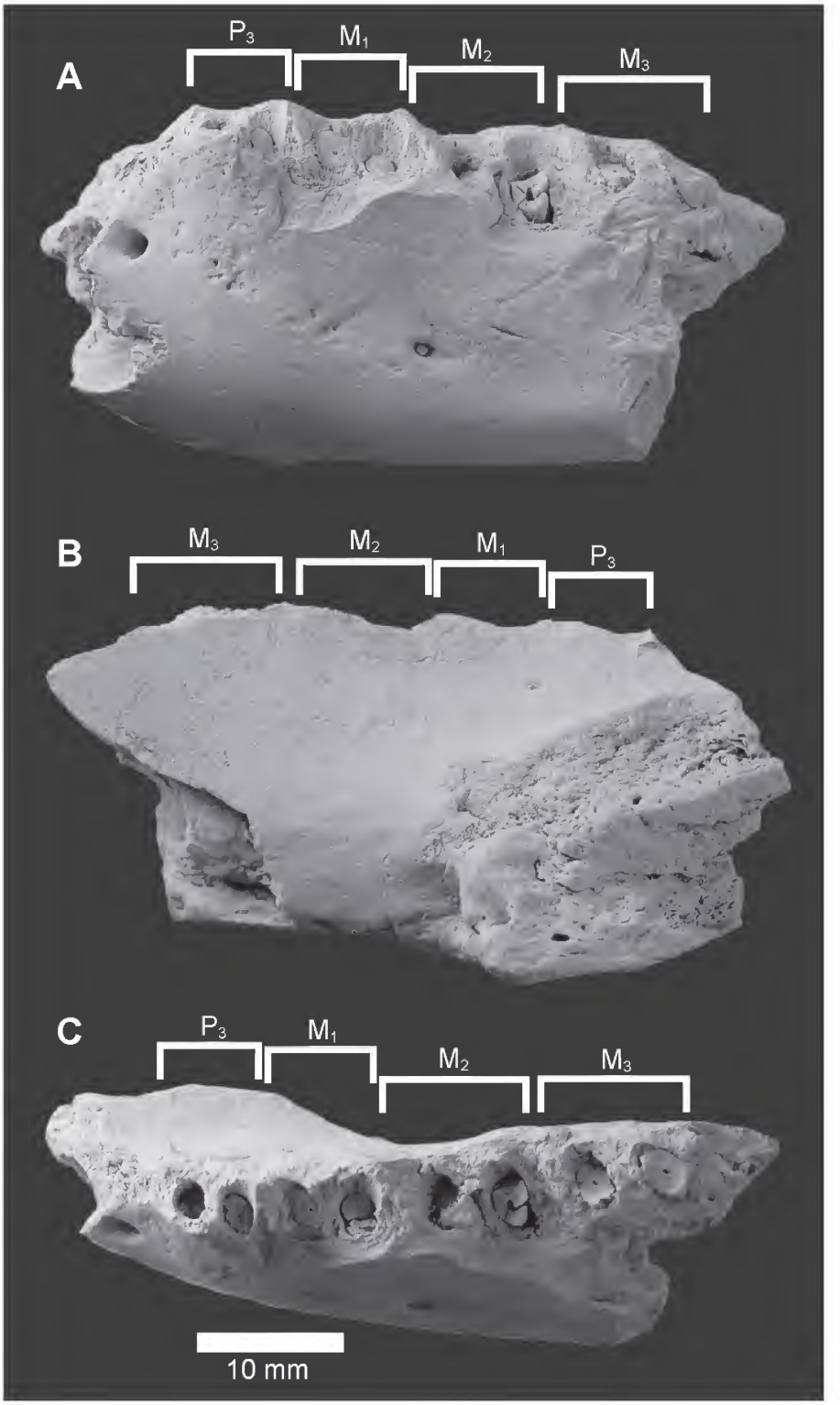

Fig. 2. Phascolarctid gen et sp. indet. dentary (QMF52287) from site QML7, Chinchilla, eastern Australia. (*A*) External view, (*B*) Internal view, and (*C*) Occlusal view.

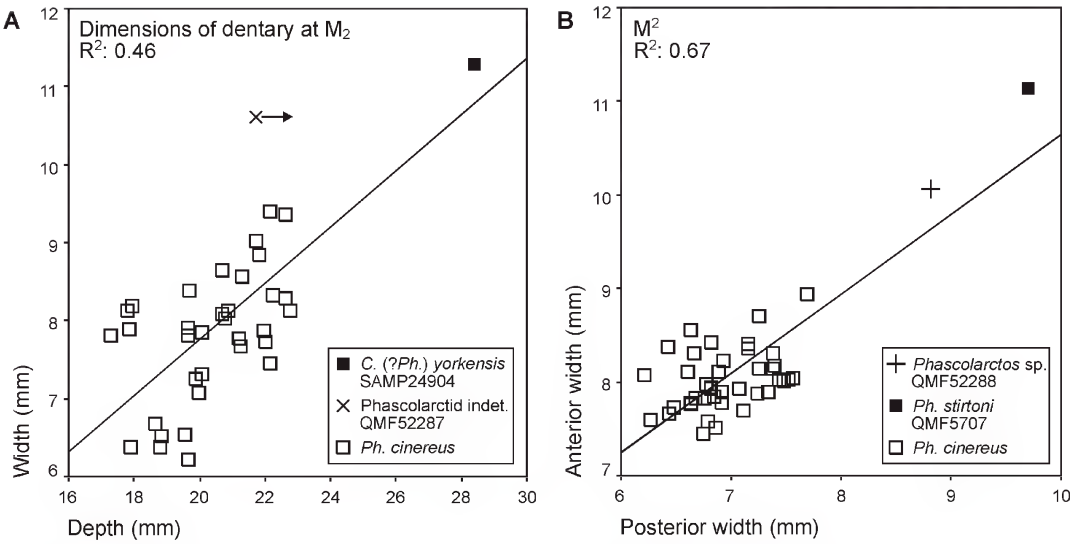

Fig. 3. Morphometrics of fossil koala specimens. (*A*) Depth versus width of dentaries of modern *Phascolarctos cinereus* from eastern Queensland (Appendix), fossil *Cundokoala* (*?Ph.*) *yorkensis* (SAMP24904) from Corra Lynn Cave (South Australia), and phascolarctid gen et. sp. indet (QMF52287) from Chinchilla, eastern Australia. Note that the depth of the Chinchilla koala dentary is a minimum measurement because the specimen is broken along the alveolar border (Fig. 2). (*B*) Anterior versus posterior width of *Phascolarctos* spp. M^2 (See Appendix for list of modern *Ph. cinereus* specimens examined).

single large pit. Comparison of QMF52287 to other large-sized phascolarctids such as *Ph. maris*, or unusual koala-like marsupials such as *Koobor*, is not possible because dentaries of those taxa are unknown.

Genus *Phascolarctos* Blainville (1816)

Diagnosis. Upper molars of *Phascolarctos* differ from all other phascolarctids (excepting *Cundokoala* (*?Ph.*) *yorkensis*) and the koala-like *Koobor* by: (*a*) being larger; (*b*) being relatively higher crowned; (*c*) by possessing well-developed molar crenulations; and (*d*) possessing well-developed ribs on lingual portion of paracone and metacone.

Phascolarctos differs from *Madakoala*, *Nimiokoala* and *Koobor* by possessing a lingual cingulum or pocket on upper molars at the crown base between the protocone and metaconule.

Phascolarctos differs from *Litokoala* and *Nimiokoala* by possessing relatively smaller neometaconules and paraconules.

Phascolaractos differs from *Madakoala*, *Perikoala*, *Cundokoala* and *Koobor* by possessing relatively smaller or weakly expressed stylar cusps, and in the case of *Cundokoala*, by possessing a relatively less-developed associated stylar shelf.

Phascolarctos differs from *Cundokoala* in being smaller and by possessing lesser-developed molar crenulations.

Phascolarctos differs from *Koobor* by: (*a*) having a square- to trapezoidal-shaped, rather than rectangular-shaped, occlusal outline; (*b*) possessing relatively longer anterior and posterior cingula; and (*c*) lacking a buccal ectoloph on the paracone.

Phascolarctos sp.

Figs 3B, 4A

Referred material. QMF52288, isolated LM^2, QML1384 (Unit "L.U."; Elephant Hole Cave), Mt. Etna, central eastern Queensland, Australia (Middle Pleistocene; Table 1)

Description. LM^2 with anterior portion missing; tooth trapezoidal in occlusal outline, tapering posteriorly; protocone and paracone sub-equal in height, slightly taller than metacone and metaconule, neometaconule shortest cusp; protocone most anterior cusp forming anterolingual corner of tooth; paracone transverse, slightly posterior to protocone, forming anterobuccal margin of tooth; metacone directly posterior to paracone forming posterobuccal corner of tooth; metaconule posterobuccal to protocone, transverse to metacone, forming posterolingual corner of tooth; postprotocrista well developed, descends posterobuccally from apex of protocone to meet with premetaconulecrista; cristae on paracone missing; rib descends posteriorly from apex of paracone to mid-crown basin; premetacrista well developed, descends anterobuccally from apex of metacone, terminating at stylar cusp D; postmetacrista well defined, descends posterobuccally from apex of metacone; posterolingual crista weakly-expressed descending from metacone apex to posterolingual base of metacone; neometaconule small, distinct at anterolingual base of metacone; premetaconulecrista well developed, descends anterobuccally from apex of metaconule terminating at midcrown basin; postmetaconulecrista well developed, descends posterobuccally from apex of metaconule, with inflexion at posterior cingulum; lingual cingulum moderately developed at base of crown between protocone and metaconule; posterior cingulum well defined, descends from inflexion with postmetaconulecrista, terminating at posterobuccal corner of tooth near stylar cusp E; metacone

buccal ridge small, descends posteriorly from stylar cusp D, terminating at posterobuccal corner of tooth; molar enamel heavily crenulated.

Remarks. QMF52288 is regarded as an M^2 due to its trapezoidal occlusal outline that tapers posteriorly and by its possession of a relatively small neometaconule, identical to that of M^2 in other species of *Phascolarctos*. QMF52288 is significantly larger than corresponding teeth of *Koobor*, *Madakoala*, *Perikoala*, *Nimiokoala* and *Litokoala*, and *Ph. cinereus*. However, the tooth is morphologically similar to other species of *Phascolarctos*. In comparison to *Ph. stirtoni*, the posterior cingula is relatively smaller, molar enamel is less crenulated (although that feature may be slightly variable judging from variation expressed in large samples of modern *Ph. cinereus*), and the tooth is smaller overall (Fig. 3B). However, judging by the range of morphometrical variation exhibited in modern *Ph. cinereus* (Fig. 3B), QMF52288 could easily fall within the lower size range of *Ph. stirtoni*. QMF52288 is somewhat similar in morphology to extant *Ph. cinereus*. However, it is larger and falls outside the morphometrical range of variation of modern populations (Fig. 3B). Pledge (1987) suggested that *Ph. maris* (a species questionable distinct from *Ph. stirtoni*; see Black, 1999) is intermediate in size between the smaller *Ph. cinereus* and larger *Ph. stirtoni*. Thus, QMF52288 potentially represents *Ph. maris*. However, it is not possible to compare QMF52288 to *Ph. maris* (nor to the significantly larger *Cundokoala (?Ph.) yorkensis*) as corresponding teeth are unknown in those species.

Phascolarctos stirtoni Bartholomai, 1968

Holotype. QMF5707, right maxillary fragment with P^3, M^{1-2}, Cement Mills, Gore, southeastern Queensland (Late Pleistocene; Price *et al.*, 2009).

Diagnosis. See Bartholomai (1968).

Phascolarctos ?stirtoni

Figs 4B, C

Referred material. QMF52289, isolated $RM^{1, 2 \text{ or } 3}$ fragment, QML7, Chinchilla, southeast Queensland, Australia (Middle Pliocene); QMF52290 isolated RM^2 fragment, QML1420 Marmor Quarry, central eastern Queensland, Australia (Middle Pleistocene; Table 1).

Description. $RM^{1, 2 \text{ or } 3}$, description based on QMF52289: Metacone only major cusp preserved, very large, worn; postmetacrista moderately developed, descends apex of metacone posterobuccally to small stylar cusp E; buccal crest small but distinct, directed anteriorly from stylar cusp E, slightly ascending buccal margin of tooth; posterior cingulum large, worn; molar enamel crenulated at posterolingual base of metacone.

RM^2, description based on QMF52290: Protocone only major cusp preserved; preprotocrista well developed, descends anterobuccally to lingual portion of anterior cingulum; postprotocrista descends posterobuccally to base of protocone; rib descends protocone between pre- and postprotocristae, well developed; anterior fossette well developed at anterior base of protocone; lingual cingulum well developed, extending along lingual margin at base of protocone, ascending and terminating at lingual corner of tooth; molar enamel crenulated on all sides of protocone.

Remarks. The wear pattern on the posterior margin of the metacone molar fragment (QMF52289) is consistent with wear from abrasion with a succeeding tooth whilst still in the maxilla. This suggests that the specimen represents either an $M^{1, 2}$ or M^3, rather than an M^4 (the most posterior tooth in phascolarctids). On the basis of molar morphology, the teeth are referable to *Phascolarctos* due to: (*a*) their well-developed molar crenulations; (*b*) minor degree of development of stylar cusps and associated stylar shelf (QMF52289); (*c*) well-developed lingual cingulum (QMF52290); and (*d*) being higher-crowned than all other phascolarctids (excepting *Cundokoala (?Ph.) yorkensis*). Morphometrically, both teeth are larger than corresponding teeth of *Ph. cinereus*, but are smaller than corresponding teeth of *C. (?Ph.) yorkensis*. The protocone fragment (QMF52290) is morphologically similar to the corresponding M^2 of *Ph. stirtoni*, particularly in the development of the anterior fossette at the base of the protocone, and the anterolingual extension of the lingual cingulum. The metacone fragment (QMF52289) lacks a well-developed stylar shelf as exhibited in *C. (?Ph.) yorkensis*, and in that respect, closely resembles the condition exhibited in *Ph. stirtoni*. Corresponding teeth of *Ph. maris* and *C. (?Ph.) yorkensis* are either not known or are poorly represented, thus, preventing further comparison to the material described here. However, the molar fragments described here are similar in size to *Ph. stirtoni*, a species that is intermediate in size between *Ph. maris* and *C. (?Ph.) yorkensis* (Pledge, 1987, 1992). Thus, QMF52289 and QMF52290 are unlikely to be referable to those poorly known taxa. The fragmentary nature of the material precludes additional comparison to *Ph. stirtoni*.

Discussion

New koala material described here significantly extends the temporal and spatial distribution of Plio-Pleistocene koalas in Australia. Previously, Pliocene records of koalas were restricted to southern Australian deposits (i.e., Corra Lynn Cave and Waikerie). Thus, the new records from the Chinchilla Local Fauna (phascolarctid indet. and *Phascolarctos ?stirtoni*) represent a significant north-eastern geographic extension for Pliocene koalas, and provide the first unambiguous evidence for the presence of koalas in the assemblage. Similarly, new records of *Phascolarctos* from the Marmor and Mt. Etna deposits extend the northern geographic distribution of Pleistocene koalas from central eastern Australia (e.g., Price, 2008a) to northeastern central Queensland. Thus, the new koala records are important because they show that *Phascolarctos* has been closely associated with eastern Australian habitats since the Middle Pliocene.

Palaeoecology. The modern Koala, *Phascolarctos cinereus*, is mostly restricted to open forests and woodlands of eastern Australia (Moore & Foley, 2000), but has been recorded, albeit as a rare component, in rainforest communities (Williams *et al.*, 1996). Koalas are folivores and feed almost exclusively on the leaves of certain species of *Eucalyptus* (Moore & Foley, 2000). Thus, because fossil species of *Phascolarctos* such as *Ph. stirtoni*, have morphologically

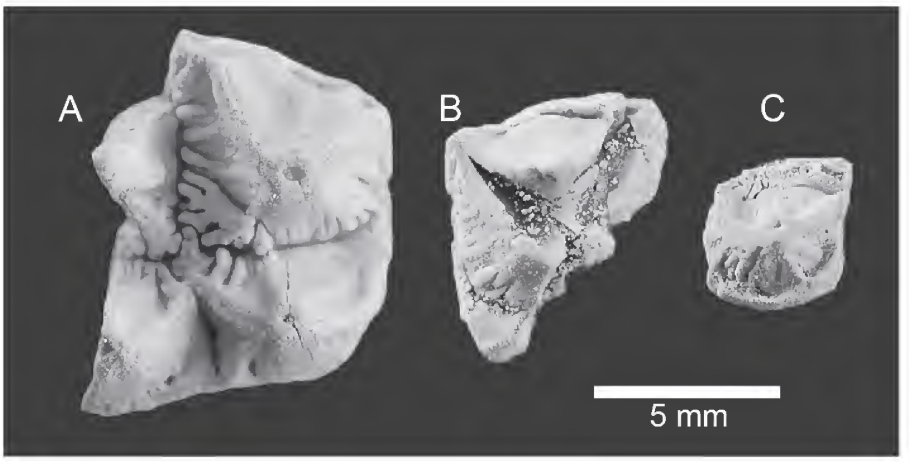

Fig. 4. Photographs of fossil koala teeth from eastern Australia. (*A*) QMF52288, LM^2 of *Phascolarctos* sp., site QML1384, Mt. Etna. (*B*) QMF52289, $RM^{1, 2 \text{ or } 3}$ metacone fragment of *Ph. ?stirtoni*, Chinchilla. (*C*) QMF52290, RM^2 protocone fragment of *Ph. ?stirtoni*, Marmor.

similar dentitions to *Ph. cinereus* (Bartholomai, 1968), the underlying assumption is that they had broadly similar habitat and dietary preferences (Archer *et al.*, 1991).

The Chinchilla Local Fauna represents a rich and diverse assemblage of fossil taxa, many of which are considered to be restricted solely to Pliocene deposits (e.g., *Euryzygoma*) (Archer, 1977b). The fauna includes molluscs, fish, lungfish, crocodiles, turtles, squamates, birds, rodents, dasyurids, bandicoots, diprotodontoids, wombats, marsupial lions, kangaroos, wallabies, and rodents (Bartholomai & Woods, 1976; Hutchinson & Mackness, 2002). The Pliocene palaeohabitat of the region was interpreted as consisting of a seasonal wetland component, with grasslands interspersed with complex and mature woodlands (Hutchinson & Mackness, 2002). The interpreted Pliocene habitat differs significantly from the habitats of the region today, which are dominated by open *Acacia* and *Eucalyptus populena* woodlands and grasslands (Fensham & Fairfax, 1997). Dawson (2004) recently described the first record of a potentially arboreal tree kangaroo from the assemblage. Thus, the identification of Phascolarctidae gen. et sp. indet. and *Phascolarctos ?stirtoni* significantly increase the known diversity of arboreal forms within the Chinchilla Local Fauna. Although the presence of such taxa provides support for the former existence of large-scale complex woodlands, they do not necessarily indicate Pliocene closed-forest in the region (Dawson, 2004). The modern Koala, *Ph. cinereus*, is extant in the region, whilst tree kangaroos are now restricted to rainforest communities in northeastern Queensland and New Guinea. Tree kangaroos are also absent from nearby intensively-sampled Late Pleistocene deposits of the eastern Darling Downs and Gore (Bartholomai, 1977; Price & Sobbe, 2005; Price & Webb, 2006; Price *et al.*, 2009). Generally, both the Late Pleistocene Darling Downs and Gore fossil faunas are dominated by terrestrial, non-arboreal, open woodland and grassland taxa (Bartholomai, 1977; Price, 2002, 2005; Price & Sobbe, 2005; Price *et al.*, 2005, 2009; Price & Webb, 2006) with very few species that also occur in Pliocene deposits (a possible exception being a species of marsupial "tapir", *Palorchestes* (Price & Hocknull, 2005)). Thus, those data suggest that significant habitat and faunal reorganization occurred in the Chinchilla region between the Pliocene and Pleistocene, presumably reflecting the contraction of dense woodlands and expansion of open woodlands and grasslands. A local reduction in habitat heterogeneity (associated with an expansion of open habitats) is also evident between the Late Pleistocene and Recent (Price & Sobbe, 2005). Therefore, those observations suggest that significant regional habitat changes have been underway since at least the Middle Pliocene.

The Middle Pleistocene Marmor (Site QML1420) faunal assemblage includes dasyurids, thylacinids, possums, marsupial lions, wombats, diprotodontoids, macropodoids, and rodents (Longman, 1925; Hocknull, 2005). The palaeohabitat is interpreted as representing a mosaic vegetation complex comprised of sclerophyll forest and grasslands based on the presence of closed forest taxa (e.g., tree kangaroos and pademelons) and open woodland taxa (e.g., grazing kangaroos and wombats) (Hocknull, 2005). The presence of *Phascolarctos ?stirtoni* supports an open woodland component of the Pleistocene habitat. The interpreted palaeohabitat differs from the modern habitat of the region, which is dominated by open woodlands and grasslands, with refugial forest and vine thickets restricted to the hillsides. Although some arboreal taxa such as tree kangaroos are now locally extinct, extant Koala populations persist in the region.

Site QML1384 (Mt. Etna, Unit "L.U.") contains a diverse faunal assemblage including squamates, turtles, dasyurids, bandicoots, possums, kangaroos, bats, and rodents. Hocknull (2005) suggested that the palaeohabitat was an angiosperm-dominated rainforest based on the presence of "specialist" extant rainforest taxa such as cuscuses (*Strigocuscus*), striped possums (*Dactylopsila*), tree kangaroos (*Dendrolagus*), and giant white-tailed rats (*Uromys*). The new record of *Phascolarctos* sp. in the assemblage suggests the possibility that a more sclerophyllous open-forest habitat type was also sampled in the deposit. That interpretation does not necessarily refute the hypothesis that the palaeohabitat was predominantly rainforest, but it does suggest that *Eucalyptus* may have formed a minor vegetative component of the palaeohabitat. Thus, the Middle Pleistocene vegetation surrounding the QML1384 "L.U." deposit may have consisted of a mosaic of habitat types. Such mosaic habitat types appear to be characteristic of many pre-Holocene Australian fossil deposits (Lundelius, 1983, 1989; Price, 2005). Alternatively, the deposit represents a significantly temporally-mixed assemblage. U/Th dating of the deposit (Table 1) provides only minimum ages of deposition and thus, the precise duration of accumulation cannot be determined. The provenance of fossil material is unclear. It is possible that different habitats occurred, and were sampled proximal to the cave over the period of deposition. However, this hypothesis cannot be tested on the basis of the data

Table 1. U-series isotopic data for eastern Australian fossil localities.

sample name	site	material	age interpretation	U (ppm)	^{232}Th (ppb)	(^{230}Th/ ^{232}Th)	(^{234}U/ ^{238}U)	(^{230}Th/^{238}U)	uncorrected ^{230}Th Age (ka)	corrected ^{230}Th Age (ka)	initial (^{234}U/ ^{238}U)
ROK27 cal	QML1384 Lower Unit	calcite filling in bone	min. age	0.0822±0.0001	7.61	38.6	1.1777±0.0024	1.1795±0.0073	333±13	332±14	1.466±0.016
ROK27 bone	QML1384 Lower Unit	macropod bone	min. age	4.6035±0.0048	15.14	1278	1.3991±0.0027	1.3856±0.0069	267±5	267±5	1.851±0.011
ROK12	QML1420 Lower Unit	tooth	min. age	13.6008±0.0291	7.32	11583.8	2.4393±0.0037	2.0554±0.0085	153.8±1.3	153.8±1.3	3.226±0.008
ROK12	QML1420 Lower Unit	calcite within tooth	min. age	0.0918±0.0001	33.16	13.4	1.8701±0.0053	1.5338±0.0299	152.3±5.7	147.8±10.9	2.461±0.055
ROK13	QML1420 Lower Unit	tooth from breccia	min. age	1.8465±0.0010	1.37	3835.6	1.3342±0.0018	0.9391±0.0029	122.9±0.7	122.9±0.7	1.4735±0.023

Note: Ratios in parentheses are activity ratios calculated from the atomic ratios, but normalized to measured values of secular-equilibrium HU-1 standard following the method of Ludwig *et al.* (1992). Errors are at 2σ level. ^{230}Th ages are calculated using Isoplot EX 2.3 (Ludwig, 1999) with decay constants $\lambda_{238} = 1.551\times10^{-10}$ yr^{-1} (for ^{238}U, $\lambda_{234} = 2.835\times10^{-6}$ yr^{-1}(for ^{234}U) and $\lambda_{230} = 9.195\times10^{-6}$ yr^{-1} (for ^{230}Th), respectively. 2σ errors in the uncorrected ages were propagated directly from the uncertainties in the (^{230}Th/^{238}U) and (^{234}U/^{238}U). The corrected (corr.) ^{230}Th age was calculated assuming the non-radiogenic U-Th component with average upper crustal ^{232}Th/^{238}U atomic ratio of 3.8±1.9 (^{230}Th, ^{234}U and ^{238}U are assumed to be in secular equilibrium). Such corrections have little impact on the ages.

currently available for site QML1384 (e.g., cave stratigraphy and dating). Regardless, the loss of Middle Pleistocene rainforests from both the Mt. Etna and Marmor regions, was likely the result of significant Middle Pleistocene climate change (Hocknull *et al.*, 2007). The local extinction of several arboreal rainforest mammals, and survival of the extant *Phascolarctos* since the Middle Pleistocene, further highlights the vulnerability of rainforest-associated faunas to vast climatic perturbations.

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Appendix. Modern *Phascolarctos cinereus* southeastern Queensland specimens examined.

registration number	location
QMJ13610	Yelarbon
QMJ15156	Jondaryan
QMJ8119	Yeronga
QMJ1350	Burleigh
QMJ992	10 miles W of Ipswich
QMJ64	Caboolture
QMJ4668	Caboolture
QMJ10972	Amberley
QMJ3404	Bribie Island
QMJ3793	Brisbane River, Bellevue
QMJ10034	Moggill
QMJ3835	Chinchilla
QMJ4370	Chinchilla
QMJ5749	Range near Brisbane
QMJ7118	Camp Mountain near Brisbane
QMJ14981	Cavern Pine Forest, Gold Coast
QMJ7240	Tamborine
QMJ8811	Toogoolawah
QMJ8353	West Burleigh
QMJ14982	Mt. Tamborine

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A Revision of the Australian Endemic Clam Shrimp Genus *Limnadopsis* Spencer & Hall (Crustacea: Branchiopoda: Spinicaudata: Limnadiidae)

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ABSTRACT. Species of *Limnadopsis* Spencer & Hall occur in temporary pools in arid and semi-arid areas of Australia. The genus is redefined and *Limnadopsium* Novojilov treated as a junior synonym. As in other spinicaudatans, most morphological characters are variable, this variability is given in expanded and rewritten descriptions of the three previously described species: *L. birchii* Baird, *L. parvispinus* Henry, and *L. tatei* Spencer & Hall. Five additional species from northern and western parts of Australia are described: *L. minuta* n.sp., *L. multilineata* n.sp., *L. occidentalis* n.sp., *L. paradoxa* n.sp., and *L. pilbarensis* n.sp. *Limnadopsis brunneus* Spencer & Hall is considered a nomen dubium. The most useful features for discriminating species are the shape of the carapace, the relative development of the dorsal carinae of the carapace, the number and relative size of the telsonic denticles, the number of spines on the cercopods, and the surface morphology of the eggs. A key is provided for all species. Western Australia has six species; much of the rest of Australia has 2–3 species, but none has been recorded from relatively well watered Victoria, Tasmania, and north Queensland.

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Of the eight genera of clam shrimps (within the Laevicaudata, Spinicaudata, and Cyclestherida) known so far from Australia, only *Limnadopsis* is endemic (Richter & Timms 2005). This genus was erected by Spencer & Hall (1896) to accommodate three new species, *L. squirei*, *L. tatei*, and *L. brunneus*. Central to their genus definition was the presence of "spinous processes on the dorsal edge of the carapace", and the presence of 26–32 pairs of legs. Sayce (1903) realized what was then known as *Estheria birchii* (of Baird 1860) was synonymous with *L. squirei*, and so designated the latter as the type of *Limnadopsis*. Henry (1924) added a new species *L. parvispinus*, but this publication went virtually unheeded (e.g., Novojilov 1958, Thiéry 1996). Much later Novojilov (1958) thought all three of Spencer & Hall's (1896) species were so different from each other that they represent three different genera, so he split off *L. tatei* into a new genus *Limnadiopsium*, but he never proposed a new genus for *L. brunneus*. Daday (1925) confused the spelling and definition of *Limnadopsis*, and this problem continues (Novojilov 1958, Straškraba 1965a, Thiéry 1996, Dumont & Negrea 2004), although Brtek (1997) corrected the spelling of *Limnadopsis, L. birchii*, and *L. squirei*. Some authors (e.g., Richter & Timms 2005) have not recognized *Limnadiopsium*, and there are problems with the descriptions of *L. parvispinus* and *L. brunneus* (Richter & Timms 2005), all of which further confuse the taxonomy of this group. The only other study on the genus is by Pabst & Richter (2004), on larval development in *L. parvispinus*.

Four undescribed species of *Limnadopsis* have been found in Western Australia, and another nearby in the Northern Territory. Given the confused state of the taxonomy of this genus and its associates, it is the aim of this paper to revise the genus.

Material and methods

Collections of *Limnadopsis* were examined in the Australian Museum, Sydney (AM), Queensland Museum, Brisbane (QM), South Australian Museum, Adelaide (SAM), National Museum of Victoria, Melbourne (NMV), Western Australian Museum, Perth (WAM), Museum and Art Gallery of the Northern Territory, Darwin (MAGNT), the corporate collections of staff of the Department of Conservation, Western Australia (DEC), and the personal collections of M.C. Geddes and the author. Information on collections is not uniform, especially for older material in museums. Measurements were made using a stereomicroscope and a template placed under the specimens and marked in half millimetres (accurate to ±0.25 mm). Drawings of whole animals, heads, and telsons were made with the aid of an ocular drawing tube. For further information on collections by the author from the Paroo region (Currawinya National Park; Bloodwood, Muella, Rockwell and Tredega Stations) see Timms & Richter (2002). Some information on collections by DEC is available in Halse *et al.* (2000) and Pinder *et al.* (2004).

Various authors (e.g., McLaughlin, 1980) have used many terms to describe the features of clam shrimps. For general body parts, I follow Richter & Timms (2005), except I use caudal claws (rather than caudal furcae) and for the claspers I follow Olesen *et al.* (1996).

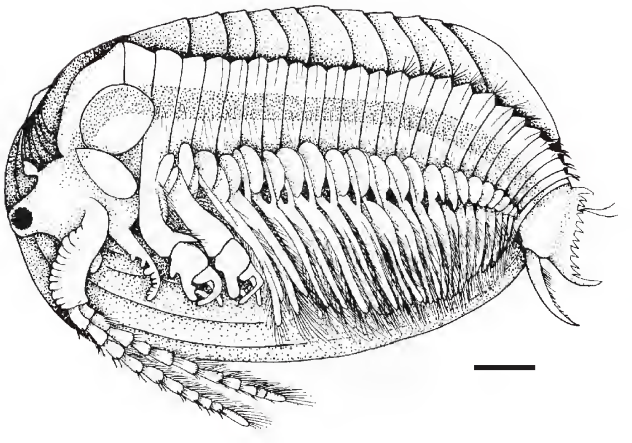

Fig. 1. General view of *Limnadopsis pilbarensis* n.sp. Drawn by Jane McRae.

Systematics

Subphylum Crustacea Brünnich, 1772

Class Branchiopoda Latreille, 1817

Order Diplostraca Gerstaecker, 1866

Suborder Spinicaudata Linder, 1945

Family Limnadiidae Baird, 1849

Genus *Limnadopsis* Spencer & Hall, 1896

Diagnosis. Umbo poorly developed, but present; carapace with many well expressed growth lines; growth lines in some species projecting as carinae along dorsal margin of carapace; head with a frontal organ on the apex of a posteriorly situated pyriform appendage; first antennae bar-shaped bearing many (5–13) lobes; 24–32 pairs of thoracopods; male with anterior-most two pairs of thoracopods modified as claspers, with the movable finger terminating in 1–3 spines, instead of a suctorial organ as in other limnadiids. First spine of the dorsal spine row of the telson large and protruding from the general alignment of the telson's dorsal surface.

Remarks

In the original diagnosis by Spencer & Hall (1896), emphasis was placed on the 10–15 clearly marked growth lines, the "dorsal line, which is raised into a much-compressed spiney keel", and the large number (26–32 pairs) of limbs. Henry (1924) and Daday (1925) continued in this vein, oblivious to the virtual lack of spiny outgrowths (i.e. carinae) and the large number (ca 30) of growth lines in *L. brunneus*. Likewise Novojilov (1958) was most impressed by the spiny dorsal outgrowths, so much so that he erected the subfamily Limnadopsinae based on this character, containing *Limnadopsis* and his *Limnadiopsium*. Straškraba (1965a), and Thiéry (1996) followed Novojilov (1958) in their definitions of the subfamily Limnadopsinae, using the spiny outgrowths as their only diagnostic feature. Given that in *L. brunneus, L. parvispinus*, and five new species described below, these spiny outgrowths are absent or minimally expressed, this character cannot be used alone as a major distinguishing feature of *Limnadopsis* or the subfamily.

Many of the other characters mentioned in the diagnosis are also not unique to *Limnadopsis*, or are not universal in the genus. However, all species of *Limnadopsis* have the first spine of the dorsal spine row of the telson large and protruding from the general alignment of the telson's dorsal surface. All species also have, well-expressed lines of growth on the carapace. However in *L. parvispinus* the lines are less well expressed than in other species, but still quite different from the few poorly expressed lines that are typical for the remainder of the Limnadiidae, except in *Metalimnadia* (Straškraba, 1965a). *Metalimnadia* differs from *Limnadopsis* in lacking a frontal organ, in having a well-developed umbo,

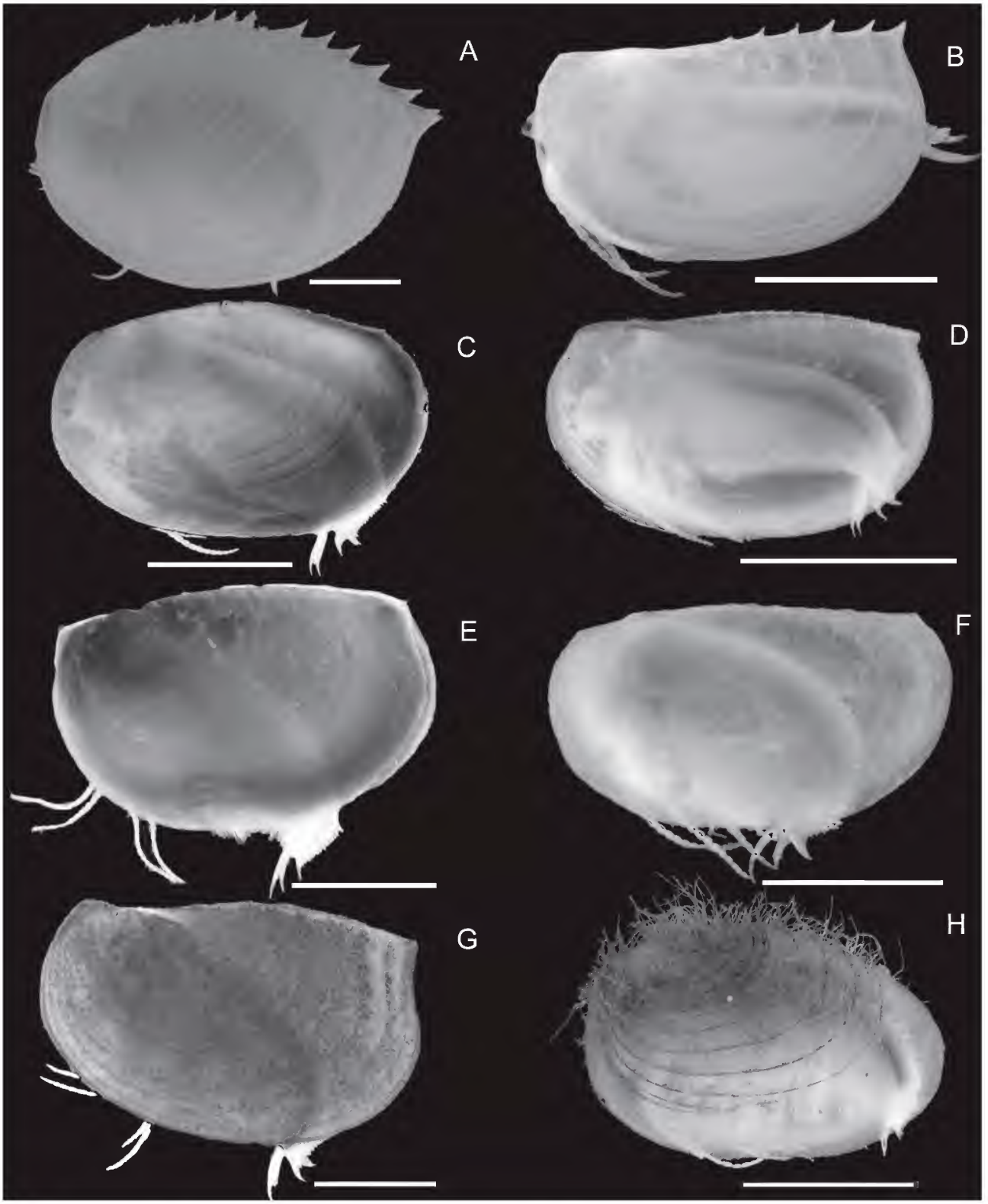

Fig. 2. Photographs of whole specimens of species of *Limnadopsis*. (*A*) *L. birchii*; (*B*) *L. tatei*; (*C*) *L. parvispinus*; (*D*) *L. minuta*; (*E*) *L. multilineata*; (*F*) *L. occidentalis*; (*G*) *L. paradoxa*; (*H*) *L. pilbarensis*. Scale bars 5 mm.

and only two lobes on the first antennae. Finally, and first introduced in the generic key provided by Richter & Timms (2005), all species of *Limnadopsis* have spines on the tip of the movable finger of the clasper, not a sucker as in other species of Limnadiidae. This unique character, together with the large and protruding first spine of the telson spine rows can be used to diagnose the genus, with limited reference as well to the numerous well-marked growth lines and dorsal carinae, The general appearance of specimens of *Limnadopsis* is shown in Figs. 1, 2.

Species descriptions

Limnadopsis birchii (Baird, 1860)

Figs. 2A, 3, 4A, 5A,B

Estheria birchii Baird, 1860: 392–393, pl. 72, fig. 1a–e; Grube, 1865: 234 (list); Simon, 1886: 453 (list).
Limnadopsis squirei Spencer & Hall, 1896: 239–241, pl. 21, fig. 15, pl. 22, figs. 16–19; Wolf, 1911: 254 (list); Dakin, 1914: 295 (list); Henry, 1924: 132 (key).
Limnadopsis birchii.—Sayce, 1903: 249–250; Wolf, 1911: 254 (list); Dakin, 1914: 295 (list); Henry, 1924: 121–122 (list), 132; Brtek, 1997: 58 (list); Richter & Timms, 2005: 349.
Limnadiopsis brichii.—Daday, 1925: 177–181, fig. 122 (misspelling); Novojilov, 1958: 104–105, fig. 13 (misspelling).

Types. None designated or available, but some material available for *L. squirei*.

Remarks on type material. Baird's (1860) material cannot be located, but some of the original material used by Spencer & Hall (1896) for their description of *L. squirei* (reported by the authors to comprise six specimens in spirit and over a 100 dried carapaces) is available. The NMV has four of the dried carapaces from central Australia which I regard as syntypes (NMV J53349), and also a few specimens in alcohol (NMV J54042), but there is uncertainly over the latter's origin so I do not treat them as syntypes.

Other material. New South Wales: 2♂, 1♀, NW of Bourke, Tredega Station, Lake Muella, 29°31'S 144°53'E, 6.xii.1999, B.V. Timms, AM P76800; 1♂, 12♀, NW of Bourke, Bloodwood Station, Last Swamp, 29°29'S. 144°49'E, 6.ii.1999, B.V. Timms, AM P76801; 5 empty carapaces, 130 km NW of Bourke, Bloodwood Station, 29.6°S 144.9°E, 26.vi.1999, S. Richter, AM P55649; 4♂, 7♀, 11 km N of White Cliffs, 30.7°S 143.1°E, no date, A.B. Chislett, AM P11456, 8♂, 5♀, W of Cooma, Coolringdon Station, Fat Hen Lake, 36°16'S 148°56'E, 19.iv.1992. B.V. Timms AM P76802. **Queensland**: near Windorah, Carranya Station, claypan, 25°18'S 142°12'E, 6.iii.1977, J. Covacevich, QM W7254; near Roma, Suva Station, Bore Hole, 26°21'S 148°28'E, 6.iii.1977, J. Covacevich, QM W10953; 2♂, E of Thargomindah, Bindegolly Lake, 28°04'S 144°10'E, 9.ii.2007, M. Handley, QM W28364; 7♂, 14♀, Cunnamulla, 28.1°S 145.7°E, iii.1947, N. Geary, AM P11794; 16 individuals, near Hungerford, Currawinya National Park, between Lakes Yumberarra and South Kaponyee, creek pool, 28°53'S 144°20'E, 7.xii.1999, B.V. Timms, QM W28365; 4♂, near Hungerford, Currawinya National Park, Lake South Kaponyee, 28°52'S 144°20'E, 7.xii.1999, B.V. Timms, QM W28366; 23 individuals, near Hungerford, Currawinya National Park, "CA" clay pan, 28°52'S 144°20'E, 3.ii.1998, B.V. Timms, QM W28368; 1♀, SW of Diranbandi, Culgoa Floodplain National Park, East Burrenbah Section, 28°51'S 146°48'E, 14.xii.1999, C. Eddie, QM W28368. **Northern Territory**: 1♂, 10♀, 3 empty carapaces, Tanami Desert Sanctuary, east of Mount Ptilotus, claypan, 20°12'S 130°12'E, no date, H. Cogger, AM P14934. **South Australia**: 1♂, 2♀, N of Oodnadatta, Hamilton Station, 17.iii.1976, Mr Cekic, SAM C6353; N of Oodnadatta, Stevenson Ck, no date but earlier than 1897, Prof Spencer, NMV J54042; N of Oodnadatta, Macumba Ck, no details, NMV J53361; Macumba & Stevenson Cks, Spencer & Hall?, NMV J53995; Cameron Corner, cane grass swamp, 22.iv.1979, M.G. & A.H. Corrick, NMV J54001; 4♂, one indeterminate individual, near South Gap homestead, South Gap Creek, i.2007, J & K Sanderson, SAM C3652. **Western Australia**: Upper

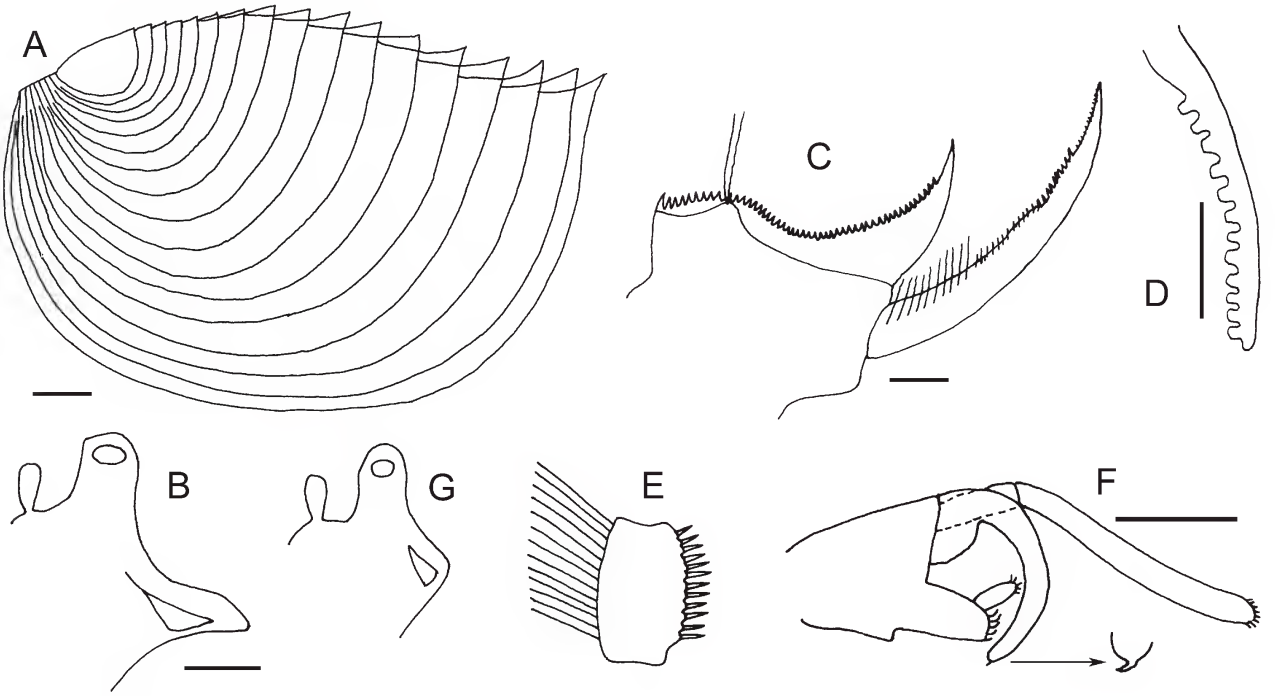

Fig. 3. *Limnadopsis birchii* (Baird), Bloodwood Station, via Bourke, NSW. Male: (*A*) carapace; (*B*) head; (*C*) telson; (*D*) antennule; (*E*) a middle flagellomere of second antenna; (*F*) second clasper. Female: (*G*) head. For clarity some growth lines of the carapace are incompletely shown anterior to umbo. Scale bars 1 mm.

Fortescue River, Mulga Downs Station, near Bunji Well, muddy pool, 22°10'S 118°26'E, 3.vii.1970, M.H. Shepherd, WAM C39325; Barrow Is., 20°52'S 115°24'E, 18.iv.1976, C. Butler, WAM C39326; near Leinster, mine site, waterhole in dry creek bed, 20.iii.2001, G. Walker, WAM C28201; 120 km NNE of Broome, "Bungnaduk", 8.ii.1989, J. Martin, WAM C39327; 1♀, NE of Carnarvon, Mardathuna Station, Bulgra pool, 24°24'S 114°33'E, 21.iii.1995, S.A. Halse, WAM C39328; 1♂, 7♀, NE of Carnarvon, Cooralya Station, Bluebush Bore Swamp, 24°28'S 114°18'E, 21.iii.1995, S.A. Halse, WAM C39329; 3♀, near Laverton, 22 km northwest on highway, samphire swamp, 28°36'S 122°13'E, 17.ii.2003, B. Datson, WAM C39330.

Distribution. Australia-wide (but not recorded from Victoria or Tasmania), generally in the arid and semiarid inland.

Comments. This large distinctive species was first described by Baird in 1860 as *Estheria birchii* on the basis of a female collected in floodplain lagoons of the Namoi (misspelt Wamoi) River, NSW. The description is poor, but there is no doubt that what is today known as *L. birchii* was the subject. In 1896 Spencer and Hall published a detailed description of a species from central Australia that they placed in a new genus and called *Limnadopsis squirei*. Sayce (1903) realized that Baird's *E. birchii* and the new *L. squirei* were synonymous. Since then, many authors (see synonymy list above) have mentioned the species, perhaps with new distribution records, but without adding to its known features.

Spencer & Hall's (1896) description is almost adequate, but it lacks a description of the thoracopods. The thoracopods of basic structure noted for spinicaudatans (McLaughlin, 1980; Alonso, 1996; Ferreri & Grygier, 2003). The male third thoracopod (Fig. 4A) with five endites on medial surface, each with differing numbers of setae (Ist with c. 20; 2nd with c. 40; 3rd with c. 30, 4th with c. 30; 5th with c. 25). These setae not evenly distributed but sparse in middle region of the endite and crowded at proximal end, more so on the 4th and 5th endites than on others. Fifth endite elongated, and similar in shape to finger-like endopod. Fifth endite bearing a one-segmented palp slightly longer than endite. Exopod bipolar with finger-like extensions distally (termed a flabellum by McLaughlin, 1980) and proximally. Endopod clothed with c. 60 setae and exopod with more than 100 setae. All setae two-segmented and differing slightly as to degree of feathering—exopod and endopod setae fully feathered, most endite setae with proximal segment sparsely feathered and distal segment densely feathered, and setae of the 5th endite naked. Oval-shaped, naked epipodite lying between proximal lobe of exopod and the main axis carrying endites. Other thoracopods essentially similar to third, but without palp on 5th endite and with slightly differing proportions of parts, particularly of epipodite. Female thoracopods similar to those of males but without palp on 5th endite, and ninth and tenth pairs with projections of exopod on which eggs carried.

Eggs (Fig. 5A,B) round, about 172 µm in diameter (range 162–186 µm, n = 10), with parallel groups of ridges and deep clefts arranged around surface. No major differences in this respect between eastern and western populations (Fig. 5A,B) studied.

Variability. *Limnadopsis birchii* is more variable than indicated by Spencer & Hall (1896). The carapace shape (Figs. 2A, 3A) is broadly oval, but usually with a distinct anterodorsal angle of about 120°, and a convex dorsal margin that is slightly depressed anterior of the umbo. The dorsal margin, posterior of the embryonic valve, bears many asymmetrical carinae (= "backwardly directed serrations" of Spencer & Hall 1896), the posterior edges of which are

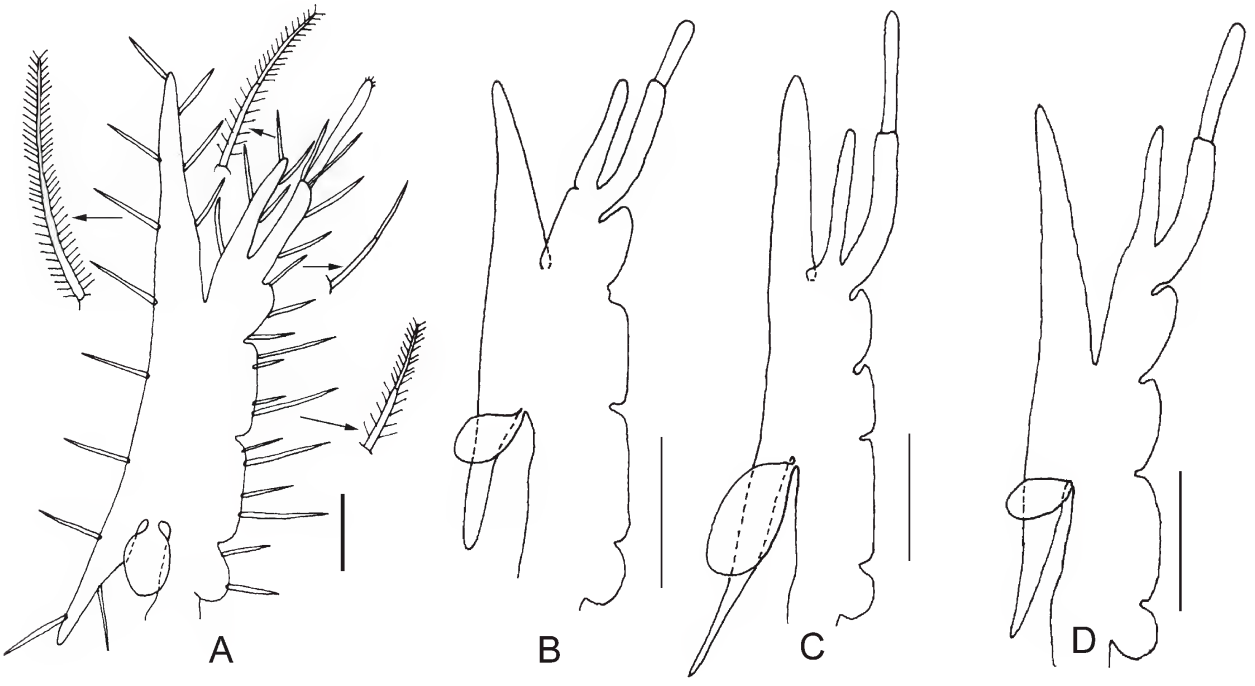

Fig. 4. Third thoracopods of males of (*A*) *L. birchii*; (*B*) *L. tatei*; (*C*) *L. parvispinus*; and (*D*) *L. paradoxa* n.sp. A few of the numerous setae (see text), and details of the major types of setae are shown only for *L. birchii*. Scale bars 1 mm.

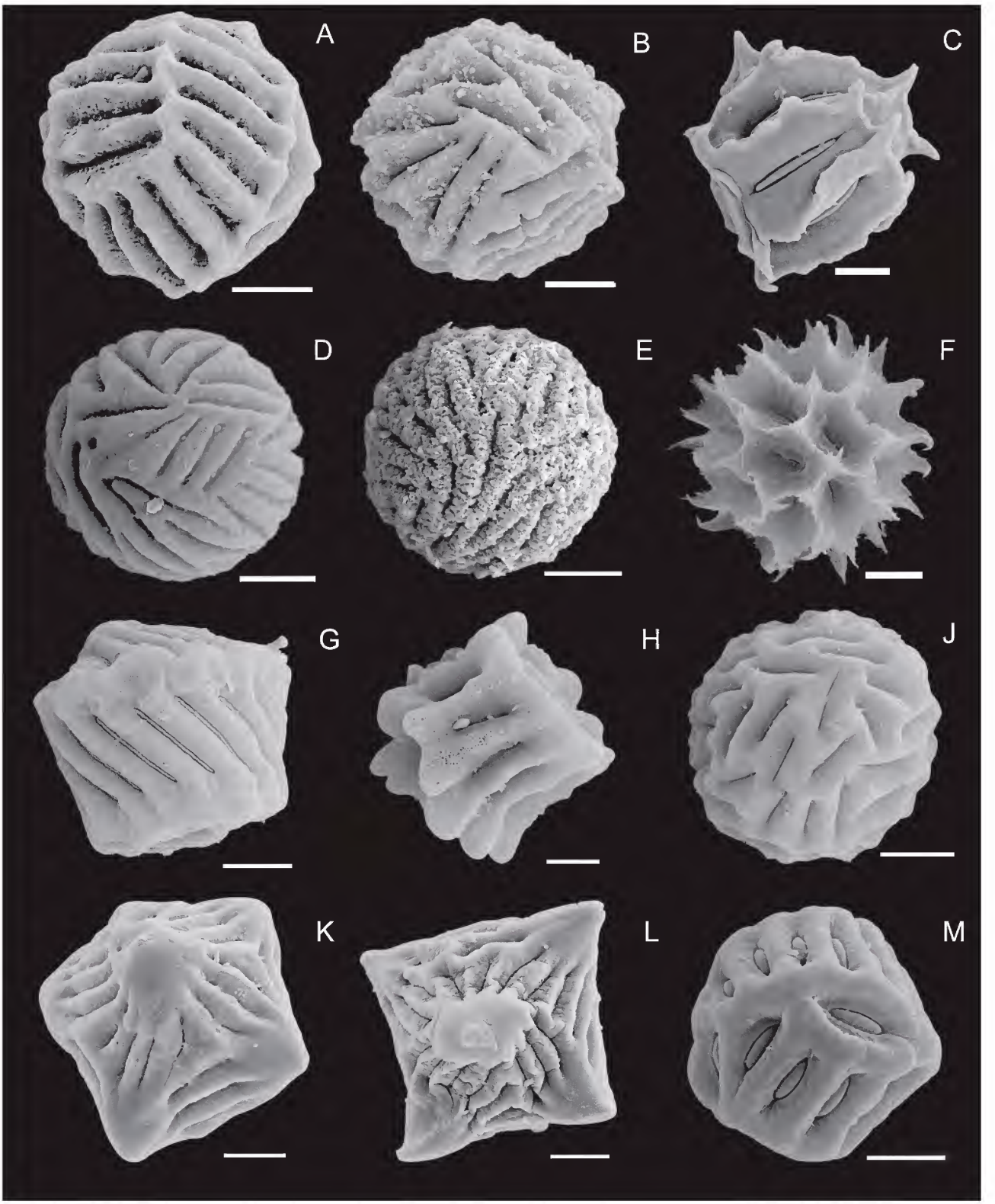

Fig. 5. SEMs of eggs. (*A*) *Limnadopsis birchii*, Twin Pans, Currawinya National Park, Qld; (*B*) *L. birchii*, Bluebush Bore Swamp, via Carnarvon, WA; (*C*) *L. multilineata*, Mitchell River Falls, Kimberley, WA; (*D*) *L. tatei*, Bloodwood Station, Paroo; (*E*) *L. tatei*, near Laverton, WA; (*F*) *L. pilbarensis*, Chichester Range, WA; (*G*) *L. parvispinus*, Bloodwood Station, via Bourke, NSW; (*H*) *L. parvispinus*, Coolringdon Station, via Cooma, NSW; (*J*) *L. occidentalis*, Boolathana Station, via Carnarvon, WA; (*K*) *L. paradoxa*, Sieda Farm, Grass Patch, WA; (*L*) *L. paradoxa*, East Lake Bryde, via Newdegate, WA; (*M*) *L. minuta*, Keep River National Park, NT. Scale bars 50 µm.

continuous with the growth lines, and which increase in size posteriorly till the last one (usually) protrudes beyond the posterodorsal corner. In many populations and individuals, however, these outgrowths are irregular and in some cases absent altogether. Similar carinae exist in *L. tatei*, but it is distinctive of *L. birchii* that invariably the protrusion of each carinae beyond the hinge line begins well forward in the previous growth area, almost back to the second preceding growth line. Generally there are about 12–13 growth lines, with a range of 11–15 mentioned by Spencer & Hall (1896), and 10–17 in the present material examined. Enormous carapace sizes of up to 27 mm long and 20 mm high were mentioned by Spencer & Hall (1896); slightly larger ones (to 29 mm) were observed in the present material and also relatively small ones of 18 mm (apparently adults). The length:depth (L:D) ratio is usually c. 1.5. Often females are slightly bigger than males, but otherwise both sexes are similarly shaped.

Spencer & Hall's (1896) description of the head and rostrum (Fig. 3B) is a little different from that observed in the present material. While in males, the rostrum is at right angles to, and anterior of the ocular tubercle, there is no sharp angle in the cephalic profile between them, as in most other species of *Limnadopsis*, but an even curvature. The rostrum is generally about equal in length and basal width, and its apex is rounded and slightly curved ventrally. In females the rostrum (Fig. 3G) is shaped like an isosceles triangle with its short axis at right angles to the head. The ocular tubercle is typically longer than wide, a shape not observed in other species of *Limnadopsis*.

The first antenna was well characterized by Spencer & Hall (1896). In males it is longer than the peduncle of the second antenna, and in females equally as long as the latter. Spencer & Hall (1896) mentioned 16 lobules in males, but the mean in the present material is 12 (Fig. 3D), with a range of 10–15. The second antennae are essentially as described by Spencer & Hall (1896), with a peduncle of 11 segments (12 in most of the present material), and 2 flagellae of about 18 flagellomeres each. Most noticeable in the present material is the large number (ca 12) of dorsal spines on most of these flagellomeres (Fig. 3E), compared to fewer than 10 in other species of *Limnadopsis*.

All specimens have 32 pairs of thoracopods, 6–8 more than in other species of *Limnadopsis*. The dorsoposterior armature on the most posterior thoracic segments, not recorded by Spencer & Hall (1896), is variable but generally consists of 3–5 spines each on the last 7–9 segments, these being preceded by 2–3 segments with both a few spines and a few setae, then another 7–10 segments with setae, the number of which decreases anteriorly in number from about 10 per segment in females, and about 5 in males, to single one. The claspers of the male (Fig. 3F) are of standard spinicaudatan structure (Fryer, 1987), with almost no macroscopic variation between populations. The asymmetrical protrusion on the anterior surface of the hand is relatively small and on the hand's proximal half. The spine on the apex of the movable finger may be single and stout, or multiple (2–4) and thin; the palp of the movable finger in the second clasper is longer than usual, being at least 1.75 to 2 times the length of the hand. Concerning the telson (Fig. 3C), Spencer & Hall (1896) mentioned that there are about 50 dorsal spines (= denticles) in each row (cf. their fig. 19), and a pair of telsonic filaments at about one quarter of its length. They described the dorsal surface curved to form a shallow S-bend, and a curved, movable caudal claw bearing a "large number of plumose setae" proximally with the distal part the dorsal edge finely setose. In the present material the mean number of dorsal telson spines in each row is indeed about 50 (range 48–55), but rarely do they increase in size posteriorly as Spencer & Hall (1896) claimed. This number is more than twice that of other species of *Limnadopsis*; furthermore the most anterior spine is little bigger than the next few, as opposed to the situation in most other species of *Limnadopsis* in which it is at least 1.5 times larger. The shallow S-bend (convex anteriorly, concave posteriorly) of the dorsal surface of the telson is present in most specimens examined, but in some the dorsal surface is almost straight. The caudal claw is evenly curved, i.e. the proximal portion is not straight as in most other species of *Limnadopsis*. It bears about 10–12 long setae (longer than width of the claw), followed in sequence by about 12–15 spines on the middle section of the caudal claw, and then the fine denticles of Spencer & Hall (1896) on the distal quarter. The most distal of the spines is almost always the largest and thickest.

Limnadopsis tatei Spencer & Hall, 1896

Figs. 2B, 4B, 5D,E, 6, 7

Limnadopsis tatei Spencer & Hall, 1896: 241, figs. 20–27; Sayce, 1903: 250; Wolf, 1911: 254 (list); Dakin, 1914: 295 (list); Henry, 1924: 122 (list), 132 (key); Richter & Timms, 2005: 349.

Limnadiopsis tatei.—Daday, 1925: 181–183, fig. 123 (misspelling of the genus name).

Limnadiopsium tatei.—Novojilov, 1958: 104, fig. 12; Brtek, 1997: 58 (list).

Types. Originally no types designated. Now a neotype (♂) has been chosen (NMV J54053).

Comments on types. The neotype is thought to be from Professor Spencer's original collection from Central Australia. Certainly its characteristics agree with the limited original description.The exact location of the type locality is unknown and even the date is not in museum records, but it is believed to be 1896. Given that this species is widespread and variable (see later), it is helpful to have a neotype taken from the type locality, illdefined as it is.

Material. **New South Wales**: 9♂, 16♀, NW of Bourke, Bloodwood Station, Shining Box Pool, 29°27'S 144°50'E, 24.v.2000, B.V. Timms, AM P76803; 6 specimens, 140 km NW of Bourke, Tredega Station, Johnsons Tank, 29°30'S 144°54'E, 26.i.1995, B.V. Timms, AM P47127. **Queensland**: 3♂, 1♀, E of Thargomindah, Bindegolly National Park, Lake Hutchinson, 1.ii.2006; 27°55'S 144°13'E, M. Handley; QM W28369; 1♂, E of Thargomindah, Bindegolly National Park, Lake Toomaroo, 17.i.2007; 27°59'S 144°12'E, M. Handley; QM W28370; 1♂, E of Thargomindah, Bindegolly National Park, Lake Bindegolly, 9.ii.2007; 28°04'S 144°12'E, M. Handley; QM W28371; 18 individuals, SW of Cunnamulla, Rockwell Station, grassy pool S of North Blue Lake, 28°51'S 144°58'E, 9.vi.2007, B.V. Timms, QM W28372; 69 individuals, near Hungerford, Currawinya National Park, the Yapunyah Swamp, 25°30'S 144°18'E, 18.v.1996, B.V. Timms, AM P47948; 5♀, near Hungerford, Currawinya

National Park, Killambirdie Waterhole, 25°48'S 144° 30'E, 8.v.1996; B.V. Timms, AM P55618. **Central Australia**: 2♂, no details, Prof Spencer, NMV J54043; 1♂, Onkaparinga Ck, no details, Prof Spencer, NMV J54053. **South Australia**: 3♂, 1♀, Olympic Dam, 30°28'S 136°44'E, 12.ii.1981, M.J. Tyler, SAM C6347; 1♀, Olympic Dam, 44 km east, 30°28'S 136°45'E, 12.ii.1987, M.J. Tyler, SAM C6348; 3♂, 3♀, Olympic Dam, 8 km on track to Lake Blanche, a samphire swamp, 30°29'S 136°48'E, M.J. Tyler, SAM C6349; 2♂, Roxby Downs, 30°42'S 136°46'E, M.C. Geddes, SAM C6350; 3♂, 96km N of Port Augusta, M. Wickstein, ii.1962, SAM C6354. **Western Australia**: Gascoyne District, Landor Station, pool near homestead, no date or collector, WAM C3485; 11 km S of Wittenoon, pools at head of Joffie Falls, 22°23'S 118°16'E, 12.vi.1970, M. Shepherd, WAM C39331; near Yalgoo, 5.x.26, J. Clark, NMV J43991; 10♂, 10♀, W of Cue, Austin Downs Station, swamp near homestead, 31.viii.2004, 27°23'S 117°45'E, B.V. Timms, WAM C39332; c. 35 individuals, near Laverton, roadside swamp 20 km west, 28°36'S 122°13'E, 22–1–2007, B.V. Timms, WAM C39333.

Distribution. Australia-wide, mainly in the central and northern inland. It is not recorded from southern NSW, Victoria, Tasmania, southern SA, or southern WA.

Description of neotype. Carapace (Fig. 6A) 12 mm by 7.6 mm, L:D ratio c. 1.6. Dorsal margin weakly curved convexly, with anterior portion depressed at umbo and slightly upturned towards dorsoanterior corner. Ten robust growth lines. Carapace dorsal surface with each growth line extended as carina. Carinae posterior to umbo large and asymmetrical and directed posteriorly, but those anterior to umbo the carinae minor and constituting small, anteriorly-facing steps in the dorsal line. Each carinae wholly contained within a single growth zone. Umbo area slightly widened anterolaterally. Carapace surface texture granular.

Head (Fig. 6B) with pyriform frontal organ situated posteriorly, preceded by a rounded ocular tubercle, and rostrum orientated at right angle to head. Rostrum length about 1.5 times its basal width; apex rounded and slightly bent posteriorly and base containing triangular naupliar eye dipping obliquely with respect to rostrum axis and occupying much of its basal area.

First antenna a little longer than second antenna peduncle, with 10 subequal lobes. Second antenna with two flagellae, each composed of about 15 beaded flagellomeres, these of variable length but generally longer and thicker proximally. Most of middle flagellomeres with 5–7 spines laterally, with no apical grouping.

Trunk segments 26. Posteriormost segment with spineless dorsal protuberance, preceding 7 segments each with 1–3 spines its protuberance; next more anterior 6 segments with long setae varying in number from many posteriorly to 1–2 on more anterior segments (Fig. 6C). Hand of claspers (Fig. 6D) with asymmetrical outgrowth on anterior edge of basal half. Immovable finger with numerous spines apically:

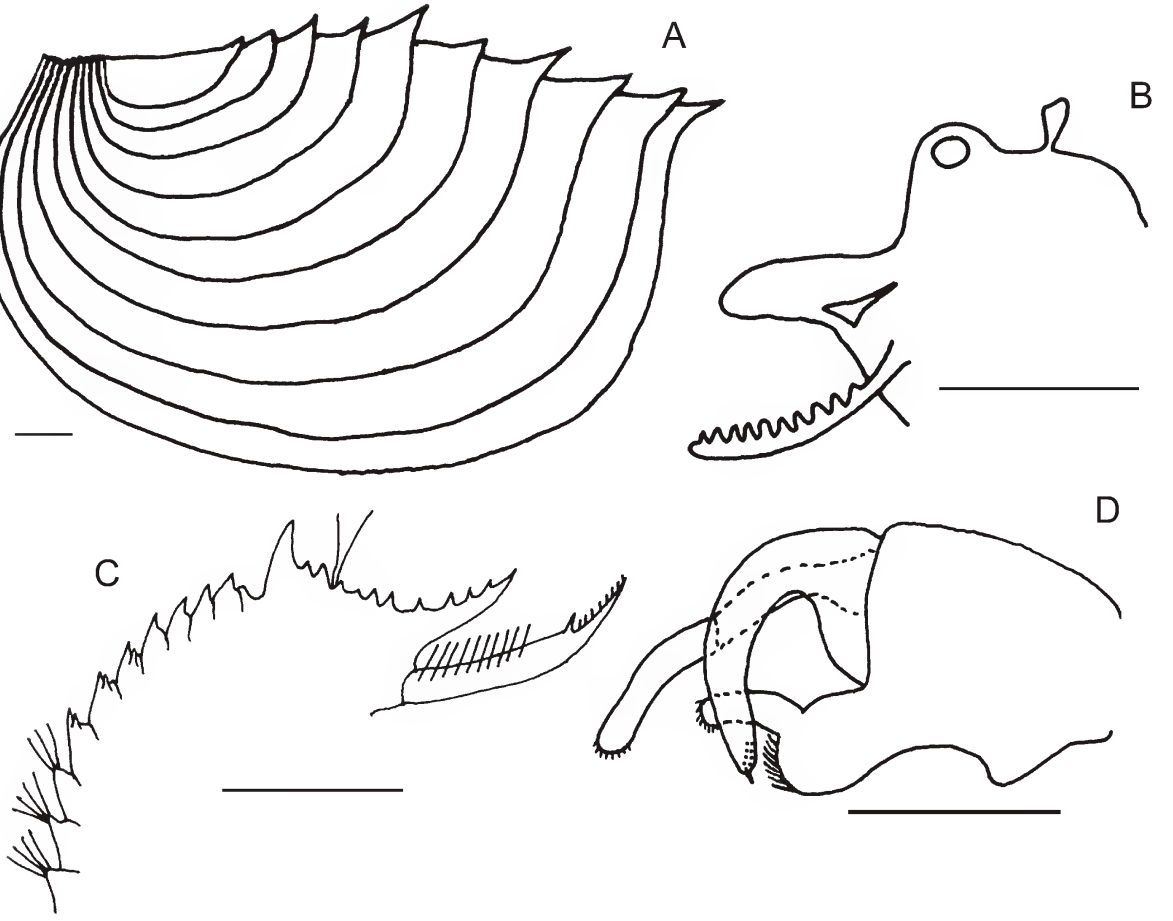

Fig. 6. *Limnadopsis tatei* Spencer & Hall, lectotype, central Australia. Male: (*A*) carapace; (*B*) head; (*C*) telson and dorsoposterior surface of trunk; (*D*) second clasper. Scale bars 1 mm.

central ones short and stout, but these changing to long, thin curved spines on inner edge. Palp of movable finger short with hair setae apically. Base of movable finger broad, supporting posteriorly an evenly curved finger terminating in a small spine. Palp two-segmented, as long as hand in the first clasper and about half as long again in second clasper. Distal segment bearing many short hair setae apically. No setae on junction of two palp segments.

Third thoracopod (Fig. 4B) similar in structure to that of *L. birchii* (Fig. 4A). Proportions of endites, endopod, exopod and epipodite slightly different, and significantly palp of the fifth endite only about half its length. Other thoracopods of same basic structure, but without palp and generally epipodite larger.

Telson (Fig. 6C) armed with 11 spines in each row, spaced unevenly and of various widths and lengths. Anterior spine about three times as large as the others and curving slightly posteriorly; posterior spine with posteriormost 3 telsonic spines on its anterior surface, curved anteriorly and more than twice as long as wide at the base. Two telsonic setae inserted on protuberance about one third of way along dorsal margin of telson. Caudal claws well developed, more than twice as large as posterior telsonic spine and unevenly curved concavely forward. Basal half thick, almost straight, and bearing about 10 shortish hair setae mesodorsally. Short spine about two-thirds of way along the claw on dorsal surface, followed by row of many denticles dorsally on pointed apex of claw.

There are no females in the original collection by Prof. Spencer, so no description of a female *L. tatei* is available.

Variability. As noted by Spencer & Hall (1896), the carapace of males varies in the shape of its dorsal outline from straight, as in the Austin Downs specimens (Fig. 7A) to slightly convex as in the neotype (Fig. 6A). Further variability is seen in size of adult male carapaces (9–13 mm long), the number of growth lines (7–11), and the development of the dorsal spines. The latter range from being almost absent, as in the specimens from Yalgoo, to well developed as in most specimens seen. The male rostrum (Fig. 7B) is often relatively longer than in the neotype, reaching twice its basal width and the degree of rounding and posterior bending very variable. First antennal lobules usually range from 8–10 and antennal segments from 12–16; both were often observed to be damaged and missing parts. Most specimens have 26 body segments, but a few have only 25. Major variability in the telson (Figs. 6C, 7C,H) includes the number of dorsal spines, ranging from 9–13, caudal claw setae varying from 8–12, and spines varying from 1–3, more often three than the one of the neotype. The anteriormost dorsal spine is always at least twice the size of other such spines, and often even larger, as in the neotype.

Females are similar to males (Fig. 7F–H), as was first noted by Spencer & Hall (1896). They noted that the dorsal margin of the carapace is distinctly more convex in the female, the rostrum is shorter, and there are fewer lobules

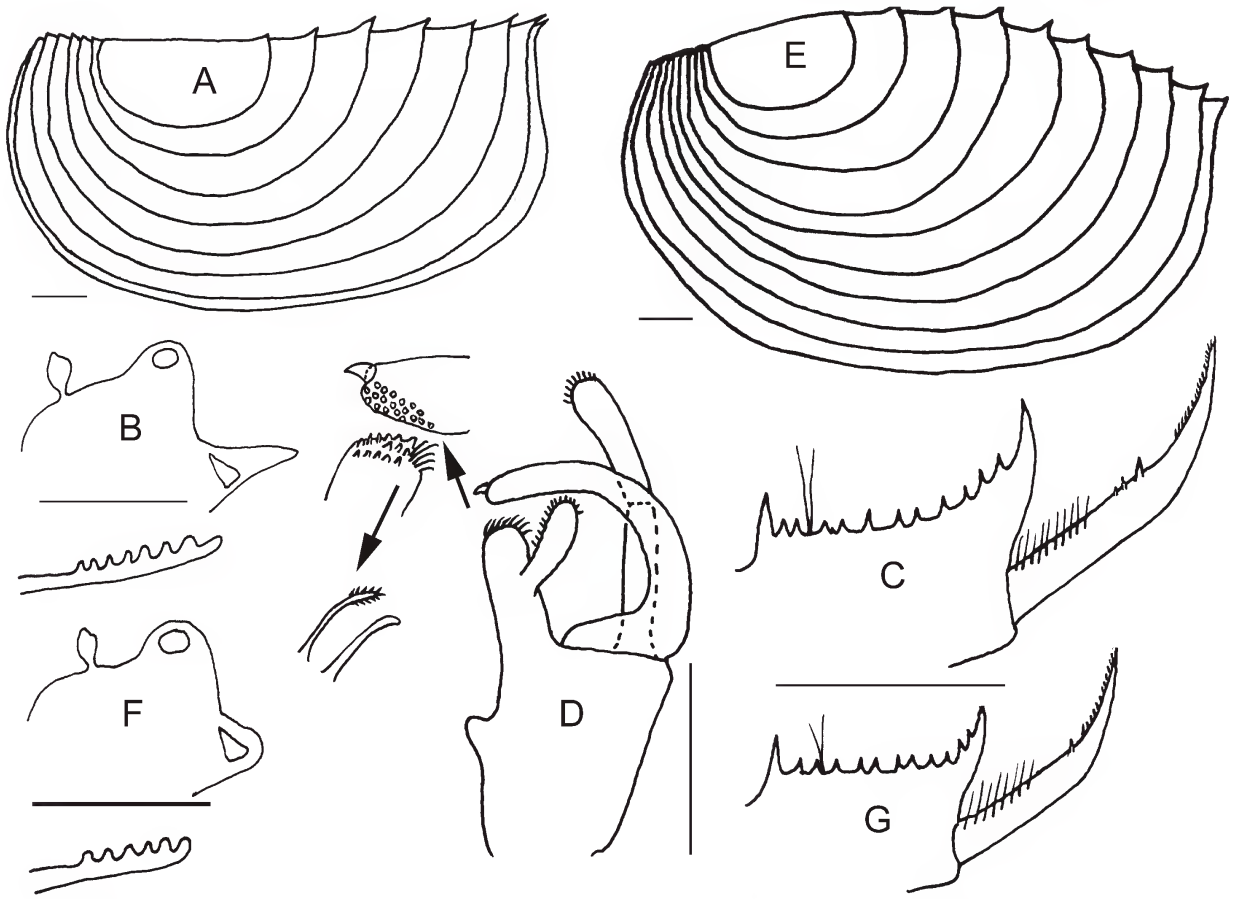

Fig. 7. *Limnadopsis tatei* Spencer & Hall, Austin Downs, via Cue, WA. Male: (*A*) carapace; (*B*) head and antenna 1; (*C*) telson; (*D*) second clasper with some details. Female: (*E*) carapace; (*F*) head and antenna 1; (*G*) telson. Scale bars 1 mm.

in the antennule than in the male. In the present material, the rostrum is as long as deep and there are about 6–8 lobules in the first antenna while the flagellomeres of the second antenna usually numbering 12–15; both figures are a little less than those of males. Number of body segments, posterodorsal armature, and the telson are similar to those in males.

Eggs. Eggs are different in the eastern and western populations studied (Fig. 3D,E). In both they are round and about 150 µm in diameter (range 144–171 µm, n = 10), and the surface has numerous straight furrows not as wide or deep as in *L. birchii*. In the western population the intervening ridges are sharper and the furrows tend to be short and arranged in short, nested Vs of 2–3 furrows, while in the eastern population, the ridges are frilly, longer and more randomly arranged. The significance of these different egg sculpturings is unknown; the eggs could be variable as in *L. parvispinus* (see later), or the differences could indicate separate species in the east and west. The later possibility is not supported by any consistent differences in the morphology of the adults.

Comment. Novojilov (1958) transferred *Limnodopsis tatei* into a new genus *Limnadiopsium* which has not been followed here (see later).

Limnadopsis parvispinus Henry, 1924

Figs. 2C, 4C, 5G,H, 8, 9

Limnadopsis parvispinus Henry, 1924: 121 (list), 132 (key), 132–133, pl. 32, figs. 1–7; Brtek, 1997: 58 (list); Richter & Timms, 2005: 349.

Types. Syntypes (3 ♂, 9 ♀) in AM G5524 and G5226.

Comment on types. The syntypes are from two different localities about 305 km apart. The inaccurate (see below) original description seems to be based on all specimens, and given the variability in this species (see below), it was decided not to choose a lectotype from a particular locality because this may jeopardize future detailed work on this species/species complex.

Material. **New South Wales**: 10♂, 10♀, 180 km NW of Bourke, Brindingabba-Willara Crossing Road, 29.3°S 144.7°E, 9.iii.1995, B.V. Timms, AM P47126; 6♂, 3♀, NW of Bourke, Bloodwood Station, Lower Crescent pool on Bell Ck, 29°32'S 144°52'E, 10.vi.1998; B.V. Timms, AM P76804; 1♂, 4♀, NW of Bourke, Bloodwood Station, Marsilea Pool, 29°33'S 144°52'E, 7.xii.1999, B.V. Timms, AM P76805; 10♂, 15♀, NW of Bourke, Tredega Station, Johnsons Tank, 29.5°S 144.9°E, 26.i.1995, B.V. Timms, AM P47124; 3♂, 9♀, NW of Bourke, Tredega Station, Johnsons Tank, 29.5°S 144.9°E, 10.iii.1995, B.V. Timms, AM P47125; 2♂, 4♀, NW of Bourke, Muella Station, vegetated pool no. 3 near homestead, 29°31'S 144°56'E, 7.xii.1999; B.V.

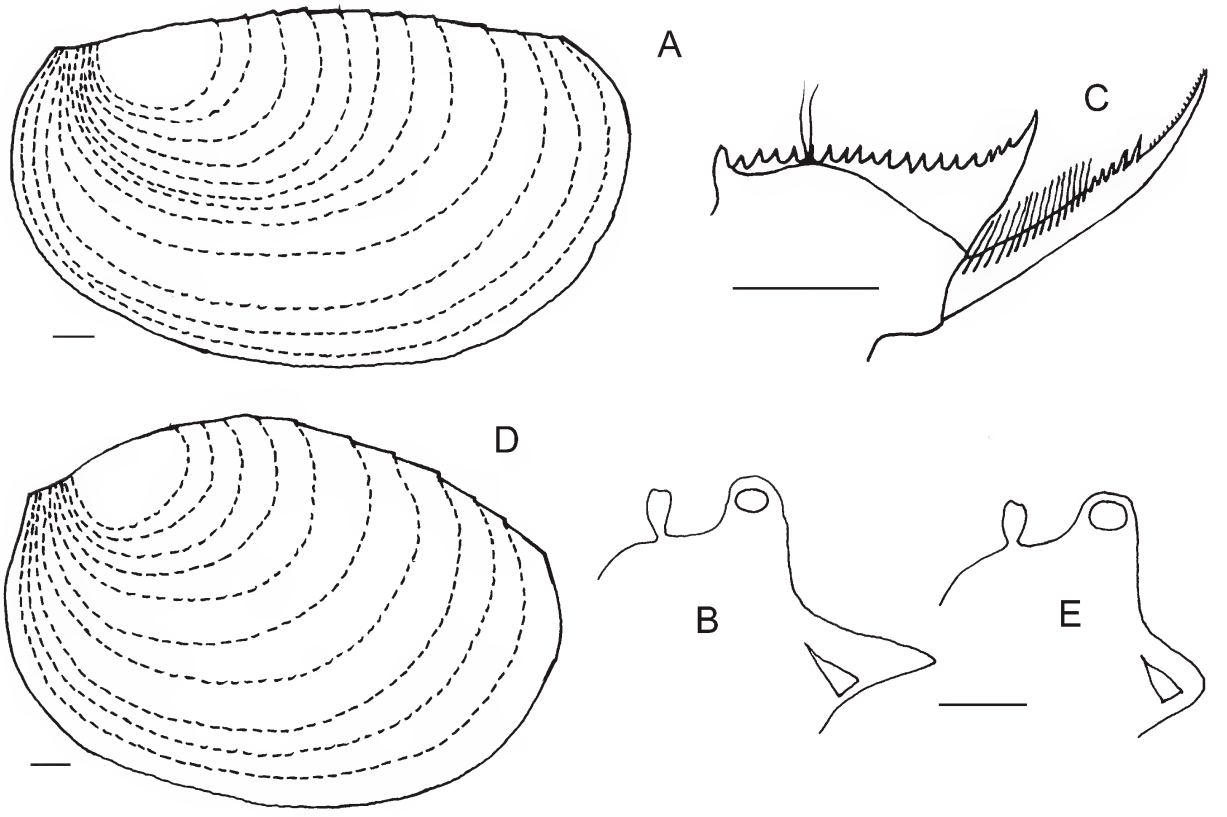

Fig. 8. *Limnadopsis parvispinus* Henry, syntypes, Mossgiel, NSW. (*A*) male carapace; (*B*) male head; (*C*) male telson; (*D*) female carapace; (*E*) female head. Scale bars 1 mm.

Timms, AM P76806; 1♀, near Trangie, Old Cathundral, 31°55'S 147°50'E, 12.ii.1941, W.R.G. Officer; 1♂, 6♀, Griffith District, Rice Bay, 34.3°S 146.0°E, 15.xi.1979, E.L. Jones, AM P53290; 13♂, 8♀, no data, P6788; 6♀, SW of Ivanhoe, Mossgiel, 33°12'S 144°36'E, no date, H.K. Bennett, AM G 5224; 3♂, 3♀, NW of Cootamundra, Bland district, 34°18'S 147°48'E, no date or collector, AM G5226; 42 individuals, W of Cooma, Coolringdon Station, Fat Hen Lake, 36°16'S 148°56'E, 19.iv.1992. B.V. Timms, AM P76807. **Queensland**: 12 individuals, S of Bollon, Bendee Station, a clearwater lake, 28°12'10"S 146°43'35"E, 23.iv.2004, S. Peck, QM W28373; 11 individuals, SW of Cunnamulla, Rockwell Station, Buster Black Box Swamp, 28°48'S 145°02'E, 9.xii.1999; B.V. Timms, QM W28374.

Distribution. Inland NSW and southern inland QLD, but could be further north, west, and south of this area.

Comments. Henry's (1924) account is sufficient to identify the species, but is inadequate on details and contains some significant inaccuracies. One of these is the claim that there are about 30 pairs of thoracopods whereas there are 25–26, and another is a supposed series of spines on the basal three-quarters of the caudal claw, whereas there is actually a mixture of a few spines apically and many setae basally. Furthermore, Henry (1924) wrote that the "the end claws are not so strongly armed" in females, whereas little difference from the situation in males, or the opposite, was observed in the syntypes. The species is redescribed below, on the basis of the syntypes.

Redescription. *Male*: Carapace (Fig. 8A) oval, generally about 15 mm long and 9 mm, L:D ratio of 1.66. Dorsal margin weakly convex and with slight depression anterior to weakly developed umbo. Both dorsoanterior and dorsoposterior angles indistinct, and anterior carapace, and particularly the posterior carapace, protruding and strongly but unevenly convex. Ventral edge weakly and evenly convex. Dorsal margin almost smooth, though with some slight serrations at posterior growth lines. Growth lines 11–12, typically weakly developed. Carapace weakly granulated within, but with smooth, somewhat lustrous, surface.

Head (Fig. 8B) with pyriform frontal organ situated posteriorly and about as high as eye mound Anterior side of eye mound and rostrum meeting at about 120°, junction evenly curved. Rostrum triangular, about 1.5 times longer than its basal width, with apex narrowly rounded and naupliar eye situated basally with its axis tipped about 45° ventrally to that of rostrum. First antenna subequal in length to peduncle of second antenna and with about 9 lobules. Second antenna with peduncle of about 12 apparent segments and flagella with 16–18 flagellomeres. Spination of middle flagellomeres variable, ranging from 4–7 spines and sometimes with two grouped apically.

Trunk segments usually 25, occasionally 26, each bearing pair of thoracopods, these decreasing in size posteriorly with anterior two modified as claspers. Posterodorsal armature with 1–3 spines on small protuberances on each of last 6–7 segments and a few setae on 4–6 segments anterior to these. Claspers of normal *Limnadopsis* structure, but with 1–3 spines apically on movable finger and prominent protrusion

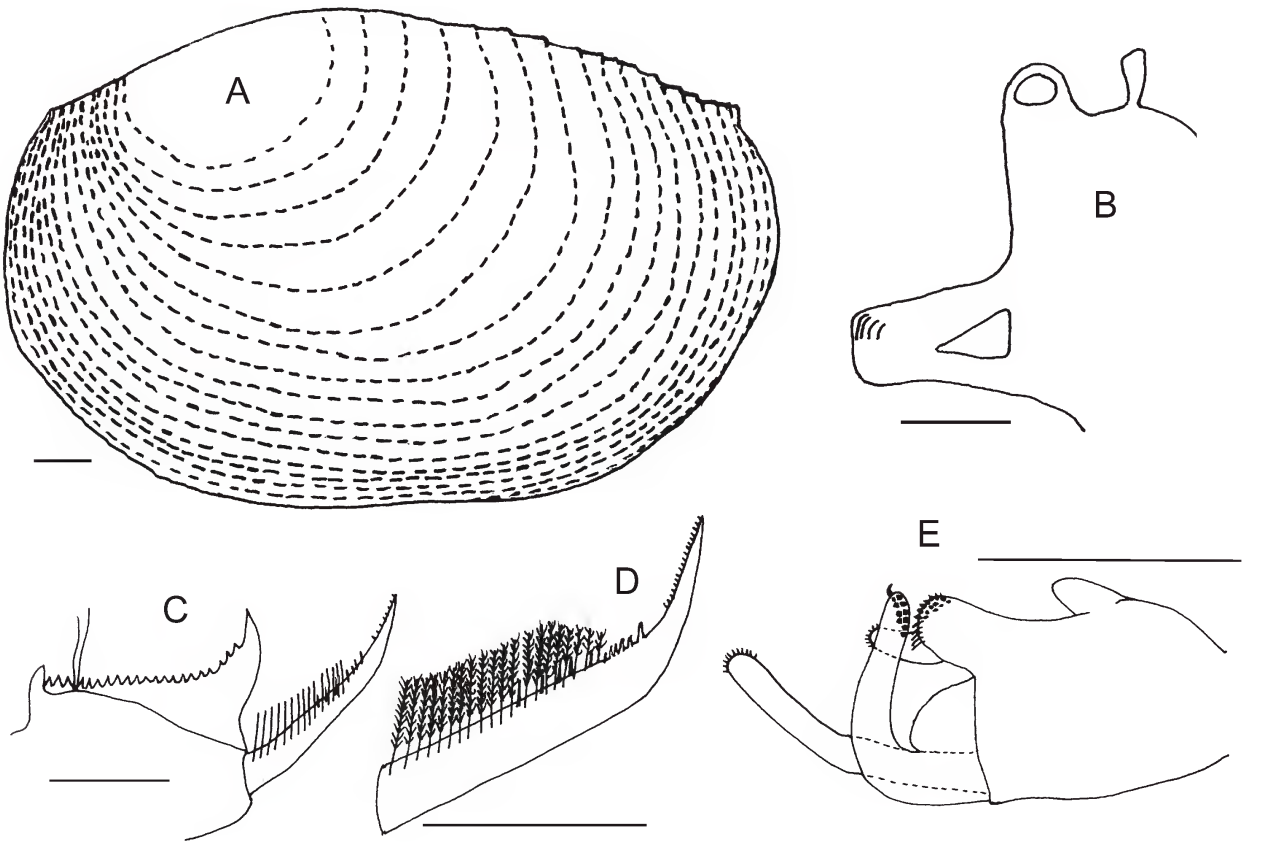

Fig. 9. *Limnadopsis parvispinus* Henry, Bollon, Qld. Male: (*A*) carapace; (*B*) head; (*C*) telson; (*D*) cercopod; (*E*) clasper. Scale bars 1 mm.

midway on the anterior edge of hand. Third thoracopod (Fig. 4C) similar in structure to that of *L. birchii*. Proportions of endites, endopod, exopod and epipodite slightly different, and significantly palp of fifth endite slightly shorter than fifth endite and epipodite proportionally larger. Other thoracopods of same basic structure, but without palp and with even larger epipodite.

Telson (Fig. 8C) with 18 dorsal spines in each row. Most anterior spine about 1.25 times larger than next few. Most spines subequal in size and evenly spaced, though most posterior ones smaller and crowded on fixed telsonic claw. Two telsonic setae inserted on protuberance situated about one quarter of way along dorsal margin of telson. Caudal claws about 8–10 times longer than wide, with long, almost straight basal section of fairly even width and much shorter, curved apical part narrowing to sharp apex. Basally each caudal claw bearing about 15 setae mediodorsally, most slightly longer than width of claw, followed by about 6 short spines almost dorsally, last of these being largest. First few spines sometimes arising from between last few setae. Curved apical part beyond last spine bearing many short denticles dorsally.

Female. Carapace (Fig. 8D) similar to that of male, but more compact (length 13–14 mm, height 9–9.5 mm) and with more convex dorsal and ventral margins. Depression anterior to umbo hardly present or not at all. Growth lines 10–11, weakly expressed.

Rostrum (Fig. 8E) a shorter isosceles triangle than in males, with basal width just greater than length. Apex rounded. First and second antennae as in male, but some of syntypes with one fewer lobe on first antennae.

Remainder of animal similar to male, except for tendency to have more spines (up to 10) on cercopods, with many of these spines mixed with last few setae.

Eggs variable (Figs. 5G,H). Most populations with eggs shaped like subconical cylinders (i.e. cupcake- or muffin-shaped) about 170 µm in diameter and height (range 168–174 µm, n = 6). Sloping sides with 16–20 parallel grooves, with narrow ridge within each groove, and low, wide ridges between, all generally sloping at about 30° from vertical axis of egg. Outer cortex with more included bubbles than in other species of *Limnadopsis*. Base generally with 2–4 parallel grooves on overall flat surface, but sometimes grooves crescent-shaped and not parallel. Dome of egg with many (4–8) grooves in parallel and grouped; highest point often off centre of vertical axis of egg. Occasionally (as in specimens from Fat Hen Lake), ridges between grooves possessing many included bubbles and dome lacking, thus egg is more cylindrical, and number of grooves on sides reduced to 10–12.

Variability. *Limnadopsis parvispinus* is a particularly variable species (cf. Figs. 8, 9). The carapace shape is reasonably standard, except for the difference in shape between males and females, but the number of growth lines in apparently mature specimens and their expression is quite variable. Generally there are about 12–15 growth lines, which are scarcely visible except near the dorsal margin. Populations with 10–12 lines occur in the Paroo, and there are 15–18 readily visible lines in individuals from Bollon. Henry (1924) gave the range as 12–14 lines, and all "well marked." Individual specimens are generally transparent and yellowish green (Henry, 1924), although those from Bollon are brown, especially near the dorsal margin.

While there is a consistent distinct difference in rostrum shape between males and females, in both sexes it is variable. In males, it may be rectangular or pointed, longer (length 2 twice depth) or shorter (length = depth), and the apex is sometimes curved ventrally. In females, it is always short and shaped like an isosceles triangle, but the height of the triangle is variable. The naupliar eye is always positioned near the base of the rostrum, but its orientation is variable, two common positions being aligned with the axis of the rostrum or with the base at a 45–60° angle to the rostrum axis. The population from Buster's Black Box Swamp, Queensland, had intersex "males" with a short rostrum and small claspers and no ordinary males.

The length of the first antenna is generally subequal to that of the peduncle of the second antenna, but in males it is slightly longer and has more lobes than in females. In males the lobes number 7–10, typically about 9, while in females the range is 7–9, with a mean of about 8. The peduncle of the second antenna typically has 12 apparent segments, while the number of flagellomeres varies from 14–21, often about 18.

Trunk segments generally number 25, but occasional specimens have 26. Posterodorsal thoracic armature in both sexes involves about the 6–7 most posterior segments each with 1–3 dorsal spines on a small protuberance, preceded by 6–7 segments with long hair-setae on similar protuberances, these decreasing in number and size anteriorly from many long setae per segment to 1–2 short setae per segment. The claspers are of standard structure for *Limnadopsis*, with the only variability noted in the spines tipping the movable finger; they are relatively small (cf. the spine in *L. tatei*) and number 1–3.

On the telson the most anterior dorsal spine in each row ranges from 1.25 times the size of the next few spines (in the syntypes) to otherwise about 1.5 times the size of the next few spines (in most specimens). Telsonic spines vary between 16 and 22 in number and are usually subequal in size and spacing, but uncommonly may be variable in both features. Almost always a few are placed on the ascending limb of the large, posterior, fixed telsonic claw. Although the caudal claws are generally long and thin (8–10 times longer than wide) with a long, straight, proximal section bearing the setae and spines, other proportions occur. The setae on the basal half of the caudal claws vary between 8 and 15 in number and generally are relatively short, particularly the last few, which often overlap with dorsal spines, situated at half to two-thirds the length of the caudal claws. These spines number 4–10 (often c. 6), with the most posterior the thickest, but not necessarily the longest. There are always many fine denticles on the dorsal surface of the curved, tapering apical part of the claw.

Limnadopsis minuta n.sp.

Figs. 2D, 5M, 10

Types. HOLOTYPE ♂ MAGNT Cr15704; allotype ♀ MAGNT Cr15705. PARATYPES 7♂, 10♀ MAGNT Cr15706 and 2♂, 2♀, AM P76809. All types: Northern Territory, E of Kununurra (WA), Keep River National Park, c. 15°57'S and 129°03'E, 8.ii.1986, M.J. Tyler, M. Davies & G. Watson.

Distribution. Known only from the type locality in the far west of the Northern Territory near the border with Western Australia.

Etymology. This species is named for its small size. At just less than 10 mm, and about the size of a typical species of *Limnadia*, it is the smallest known species of *Limnadopsis*, a genus known for its relatively large size among spinicaudatans.

Male. Carapace (Fig. 10A) 8.8 mm by 4.6 mm, L:D ratio of 1.9. Dorsal margin slightly convex and smooth, with only very minor carinae at posterior of the growth line and dorsal margin junctions. Carapace half-oval shaped with both ventral corners well rounded. Dorsoanterior angle and dorsoposterior angle both about 110° and carapace slightly expanded dorsoposteriorly. Umbo present but inconspicuous. Eighteen well expressed growth lines. Carapace surface minutely granular and uniformly brown in preserved specimens.

Head (Fig. 10B) with pyriform frontal organ behind eye mound and subequal to latter in height. Anterior surface of head and rostrum meeting at sharp angle, c. 110°. Rostrum about as long as frontal surface of head, slightly downturned at apex and containing triangular naupliar eye lying in a similar axis. First antenna a little longer than peduncle of second antenna with 8 lobules. Second antenna with peduncle of 12 apparent segments, many with numerous spines dorsally, and with two flagella of 18–20 flagellomeres. Most flagellomeres, particularly those in middle region of each flagellum (Fig. 10E), with c. 4 spines on anterior margin, usually with 2 (rarely 3) crowded apically and with the proximal surface bare.

Trunk segments 24, each bearing a pair of thoracopods, these decreasing in size posteriorly and the anterior two pairs modified as claspers. Posterior dorsal armature of 3–5 spines on small protuberances on about last 6 segments, many long setae on the 5 or so segments preceding these and a few setae on the next 4 or so more anterior segments. Claspers (Fig. 10D) of normal structure for *Limnadopsis*, with one spine apically on movable finger and asymmetrical protrusion near the base of anterior edge of hand.

Telson (Fig. 10C) with two rows of 17 dorsal spines, all sharp and varying a little in size. First spine about 1.5 times larger than the next few spines. Dorsal surface between lateral spinous rows with anterior hump on which telsonic setae are inserted, followed posteriorly by marked depression as surface generally evenly slopes to caudal claw articulations. Caudal claw about 8 times longer than wide, with long, almost straight, basal section of even width and much shorter, curved, apical part narrowing tosharp apex. Caudal claw basally with about 12–15 setae mediodorsally, most a little longer than its width, followed by 3–5 short spines inserted almost dorsally, posteriormost of these being by far (3×) the largest. Curved tapering apical part bearing many short denticles dorsally. Ventroposterior corner of telson with a spinous projection.

Female. Very similar to male. Carapace slightly larger, 9.2 mm by 5.1 mm, L:D ratio of 1.86, dorsal margin slightly curved. Head (Fig. 10F) with typical short rostrum of female *Limnadopsis*. First antenna with 6 lobules. Telson (Fig. 10G) as in male and both the features peculiar to this species: depression in the dorsal surface posterior to telsonic filament mound, and spiniform projection at ventroposterior corner.

Eggs (Fig. 45K) rounded polyhedral, about 160 µm in diameter (range 153–168 µm; n = 5). Each surface of polyhedron consisting of 1–3 oval grooves, each groove containing low longitudinal ridge internally and surrounded by high,

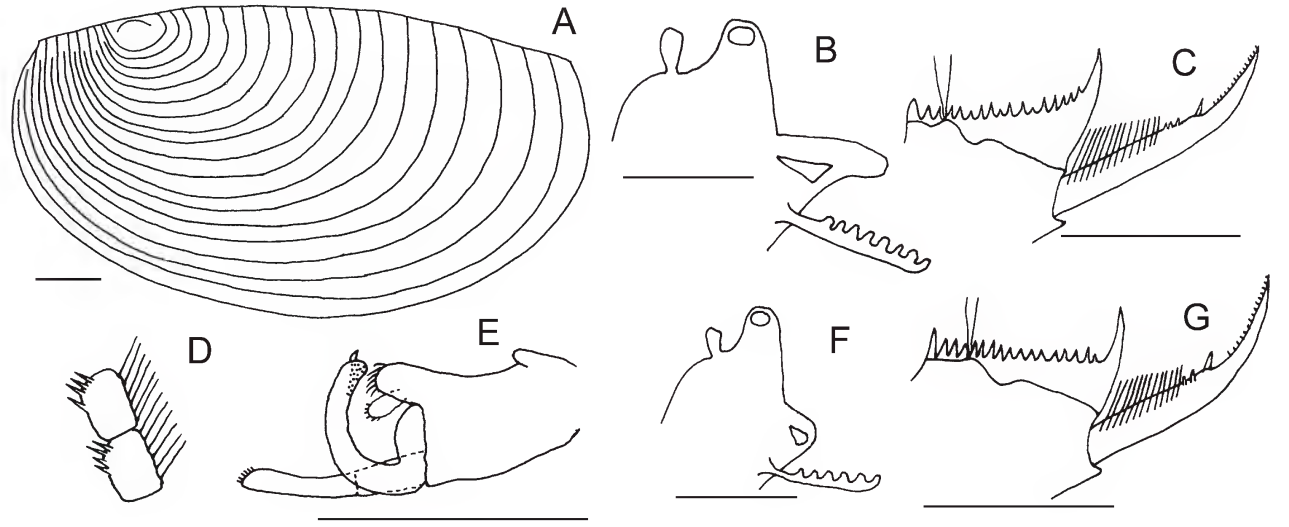

Fig. 10. *Limnadopsis minuta* n.sp., Keep River National Park, NT. Male: (*A*) carapace; (*B*) head; (*C*) telson; (*D*) a middle flagellomere of second antenna; (*E*) clasper. Female: (*F*) head; (*G*) telson. For clarity some growth lines of the carapace are incompletely shown anterior to umbo. Scale bars 1 mm.

rounded ridge, these meeting end-to-end in rounded protrusions. Either series of such protrusions or ridges forming edges of each polygon.

Comments. Other specimens in the single collection available show little variation from the type material. No other species of *Limnadiopsis* is so small yet has 18–19 growth lines, nor such a high L:D ratio, only 24 trunk segments, a spinous projection on the ventroposterior corner of the telson, a depression in the dorsal surface of the telson, and the unique egg characteristics. Overall, *L. minuta* is reminiscent of *L. tatei*, but it lacks the dorsal carinae of the carapace of *L. tatei* (although sometimes these are absent in *L. tatei*, too), the carapace shape is similar in males and females in *L. minuta*, its telsonic spines are more numerous and less variable in size and position than those of *L. tatei*, and there are fewer spines on the caudal claw in *L. tatei*. It is perhaps tempting to consider *L. minuta* as comprising juveniles of *L. multilineata* n.sp. (see below), especially given the superficially similar telsons and the large number of growth lines, but this is not possible in light of the markedly convex dorsal margin of the carapace in females of *L. multilineata*; the presence of a conspicuous ventroposterior expansion of the carapace and lack of a ventroposterior spinous outgrowth of the telson in that species; different spination of the antennal rami; and the completely different egg structure.

Limnadopsis multilineata n.sp.

Figs. 2E, 5C, 11

Types. Holotype ♂WAM C39334; allotype ♀WAM C39335, paratypes WAM C38102. Type locality: Western Australia, Kimberley, Mitchell Falls, rock pools at the top. 14°49'S 125°42'E, 14.i.1973, Smith-Johnstone.

Other material. **Western Australia**: via Broome, Lake Campion, 17°50'S 122°45'E, 28.iii.1996, C. Brockway, WAM C38103.

Distribution. Kimberley and adjacent area of northwestern Western Australia.

Etymology. The specific name refers to the large number of growth lines in this species.

Male. Carapace of mature individuals (Fig. 11A) about 10–12 mm long and 6–8 mm high, L:D ratio c. 1.5–1.6. Dorsal margin almost smooth and nearly straight, anterior angle distinct, about 100°, and dorsoposterior margin slightly depressed and ending in rounded protrusion. Umbo distinct, triangular in shape, but not protruding above the dorsal margin. Anterior edge of carapace evenly curved, ventral edge almost straight, and posterior edge protruding and rounded so that it is convex posteroventrally and concave dorsoposteriorly. About 20 distinct growth lines with a further 10–12 closely spaced lines on outer 10–15% of carapace. Carapace brown and surface apparently granular, but "grains" actually comprising numerous dendritic pigment cells.

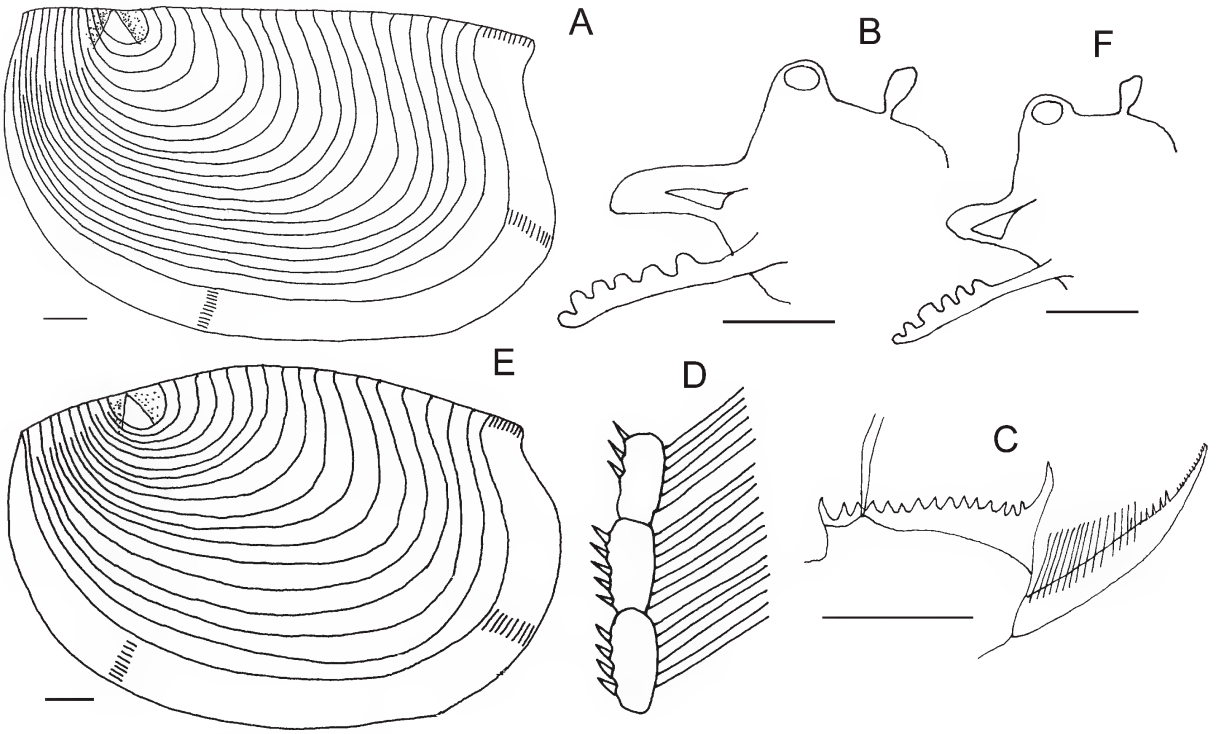

Fig. 11. *Limnadopsis multilineata* n.sp., Mitchell Falls, Kimberley, WA. Male: (*A*) carapace; (*B*) head; (*C*) telson; (*D*) a middle flagellomere of second antenna. Female: (*E*) carapace; (*F*) head. For clarity, some growth lines are incompletely shown anterior to umbo and marginally. Scale bars 1 mm.

Head (Fig. 11B) with pyriform frontal organ placed posteriorly and protruding a little farther than eye mound. Anteriorside of eye mound and rostrum meeting at about 120°, junction angular. Rostrum protruding with almost parallel dorsal and ventral edges and downward curving apex. Naupliar eye triangular with largest surface ventral. First antenna subequal in length to peduncle of second antenna and having about six lobules. Second antenna with peduncle of 12 apparent segments and two flagella of about 20 flagellomeres each. Most second antennal segments, particularly in the region of each flagellum, bearing 3–5 spines anteriorly (Fig. 11D).

Trunk segments usually 26, each bearing pair of thoracopods, these decreasing in size posteriorly and with anterior two pairs modified as claspers. Posterodorsally each segment with large, rounded protuberance, this bearing 5–7 large spines on last five segments, many setae on next 5 segments anterior to these, and 1–3 setae on most other segments. Claspers of normal structure for *Limnadopsis*, with single spine apically on movable finger.

Telson (Fig. 11C) with about 15 spines in each dorsal row, largely saw-tooth in appearance, i.e. shaped like isosceles triangles, but first two narrower, first a little longer than second. Two telsonic setae inserted on protuberance situated about one fifth of way along dorsal side of telson. Caudal claws about 9–10 times longer than wide, fairly evenly curved ventrally and bearing about 14–18 setae mediodorsally, followed by about 6 short spines dorsally and numerous denticles on the markedly curved apical quarter of claw. First one or two spines sometimes arising between last few setae.

Female. Largely similar to male, except in carapace shape (Fig. 11E), rostrum shape (Fig. 11F), and lack of claspers. Dorsal margin of carapace evenly arched, almost smooth. Dorsoanterior angle distinct, about 110°, dorsoposterior angle as in male, but not so marked. Umbo as in male. Anteroventral area of carapace more convex than in male, while posteroventral area also expanded as in male but more posteriorly than ventrally, thus giving an appearance of greater posterior expansion than in male. Growth lines as in male.

Head (Fig. 11F) with proportionally smaller eye than in male, and thus with pyriform frontal organ protruding more dorsally than in male. Rostrum short, almost in form of isosceles triangle, with rounded apex. Naupliar eye triangular and occupying about half of rostrum.

Eggs (Fig. 5C) most unusually shaped and structured; somewhat bell-shaped, about 240 µm high and about 220 µm in diameter (range 236–242 µm high, 218–223 in diameter, n = 5), with about 7 (6 around the circumference and one ventrally) large grooves separated by unevenly developed sharp ridges, some of latter meeting at top in distinct point. Each groove containing smooth, weakly developed subsidiary ridge.

Variability. Specimens from Broome are a little different from the type lot. The carapace tends to be slightly larger at 11–12 mm by 7–8 mm, but the unusual shape is the same as in males and females from Kimberley. The dorsal margin is more irregular than in the Kimberley specimens, but still basically smooth. There are only 25 growth lines, with nearly 20 of these distinct and well spaced and 4–6 situated marginally and closely spaced; therefore they do at least feature the same unusual arrangement of many well-spaced lines and a few tightly-spaced lines. The first antennae have 7 lobules and the second antenna 18 flagellomeres, both figures being slightly different from the type lot. The telson also armed differently: 16–18 dorsal spines with the first one 1.5 times larger than the rest, and caudal claw with about 15 long setae and 4–5 spines two-thirds of the way along its length.

Comments. This species is distinctive by reason of its carapace shape and its possession of numerous growth lines arranged in two groups about 20 normally spaced lines and 4–10 marginal lines spaced very closely together. It has many (ca 5–6) spines midlength on the cercopods, as do *L. parvispinus, L. occidentalis* and *L. minuta*, but is easily distinguished from these species by its unique carapace as mentioned above, and in contrast to *L. parvispinus* and *L. occidentalis*, by the well expressed growth lines (as opposed to faint lines), and 1–2 fewer spines on the middle flagellomeres. Features distinguishing it from *L. minuta* are noted above.

Limnadopsis occidentalis n.sp.

Figs. 2F, 5J, 12

Types. Holotype ♂ WAM C39336, allotype ♀ WAM C39337, paratypes, 2♂, 2♀, WAM C39338. Type locality: Western Australia, N of Carnarvon, Boolathana Station, unnamed claypan, 24°38'34"S 113°59'35"E, 15.iii.1995, S.A. Halse.

Other material: **Western Australia**: 2♂, 8♀, 58.6 km south of Roebourne, small pools adjacent to creek, 20°48'S 117° 6'E, 25.vi.1964, C. Pugh, AM P55651; 1♂, 131 mile post, road to Port Headland via Woodstock, waterhole, 21°12'S 118°48'E, 26.vi.1964, C. Pugh, AM P55650; 6♂, 2♀, E of Kalbarri, Coolcalalaya Station, unnamed clay pan, 27°31'29"S 115°05'14"E, S.A. Halse, 15.iii.1995, WAM C39339; c. 40 km south of Mullewa, Tardan, Christian Brothers College, dam, 28°43'S 115°49'E, 25.vii.1999, J. McRae & A. Pinder, DEC, Woodvale, SPS185; 1♀, via Laverton, 20 km west near highway, samphire swamp, 28°36'S 122°13'E, 17.ii.2003, B. Datson, WAM C39340.

Habitat and distribution. *Limnadopsis occidentalis* lives in a variety of temporary fresh waters, including claypans and floodplain pools, all in northwestern Western Australia.

Etymology. The species name is derived from the Latin *occidens* referring to the direction of the setting sun, and hence "west" an appropriate epithet for a species found in the west of Australia as opposed to its closely related species *L. parvispinus*, which is found in eastern Australia.

Male. Carapace (Fig. 12A) oval, 11 mm by 6 mm, L:D ratio = 1.8. Dorsal margin weakly convex with highest point at about one-third length, slight depression anterior to umbo and distinct dorsoposterior angle. Dorsal margin almost smooth, but with slight serrations at many growth lines, mainly posteriorly. Growth lines 11, weakly expressed. Carapace weakly granulated within, but presenting a smooth yellow-buff surface in preserved condition.

Head (Fig. 12B) with pyriform organ posterior to eye mound and about as high as latter. Anterior sides of eye mound and rostrum both straight and meeting at a distinct angle of about 110°. Rostrum elongated triangular, about as long as anterior surface of head, apex rounded and slightly flexed downward. Naupliar eye triangular, its axis aligned similarly to that of rostrum. Length of first antenna subequal to that of peduncle of second antenna, and former bearing 7 lobules. Second antenna with 12 apparent peduncular segments and 15–16 flagellomeres on flagella, most middle segments with 5–7 spines, 2 of which sometimes grouped apically.

Trunk segments 25 in number, each bearing pair of thoracopods, these decreasing in size posteriorly, and anterior two pairs modified as claspers. Posterior dorsal armature comprising 1–3 spines on small protuberances on each of last 7 segments, and a few setae on preceding 6 segments. Claspers of normal structure for *Limnadopsis*, with one spine apically on the movable finger, and prominent, asymmetrical protrusion midway along anterior edge of hand.

Telson (Fig. 12C) with two rows of 13 dorsal spines each. Most anterior spine about 1.5 times the size of next spine, most posterior spines smaller and sharper than anterior spines, and spines in middle of row more widely spaced than anterior or posterior spines. Two telsonic setae inserted on protuberance situated about one quarter of way along dorsal side of telson. Caudal claws about 8 times longer than wide, with long, almost straight basal section of even width and much shorter, curved apical part tapering to a sharp apex. Basally, cercopods bearing about 12 setae mediodorsally, most of them being a little longer than width of claw, followed by 3 short spines inserted almost dorsally, the posteriormost the largest. Curved, tapered apical part of cercopods bearing many short denticles dorsally.

Female. Carapace (Fig. 12D) oval, 11 mm by 7 mm, L:D ratio 1.57. Dorsal margin more convex than in male and also with distinct depression in umbo area. Dorsal margin largely smooth, but minor serrations present posteriorly at junctions of growth lines. Growth lines 9, weakly expressed.

Head (Fig. 12E) typical for females of *Limnadopsis*, with short triangular rostrum. Six lobules on first antenna. Second antenna as in male.

Telson (Fig. 12F) similar to that of male, but with 15 telsonic spines in each row, and six spines on caudal claws.

Eggs (Fig. 5J) round, about 175 µm in diameter (range 170–178 µm; n = 5) with short deep grooves, aligned at most in pairs, otherwise set at various angles to one another. Intergroove areas smooth and internally frothy.

Variability. Considerable variability was noted in representatives of the six populations studied. Growth lines vary from 9 to12, but they are invariably weakly expressed and meet the dorsal margin in at most weak dorsal serrations posteriorly. First antennal lobules vary from 6 to 9, with males of a given population generally having one more than females. On the telson, the dorsal spines vary from 12 to16 per row, with a mean of 13; and the spines on the caudal claws range from 2 to 6, usually about 4.

Comments. This species is similar to *L. parvispinus*. Despite wide variation in many features of both species, there are many differences between the two, including: (*a*) fewer telsonic spines in *L. occidentalis* (about 13–15 per row compared to about 18–22); (*b*) A slight anterior depression in the dorsal carapace margin of *L. occidentalis* while in *L. parvispinus* the margin is straight or slightly convex; (*c*) the differently shaped eggs, round in *L. occidentalis* and with the grooves ungrouped or at most in pairs, compared to cy-

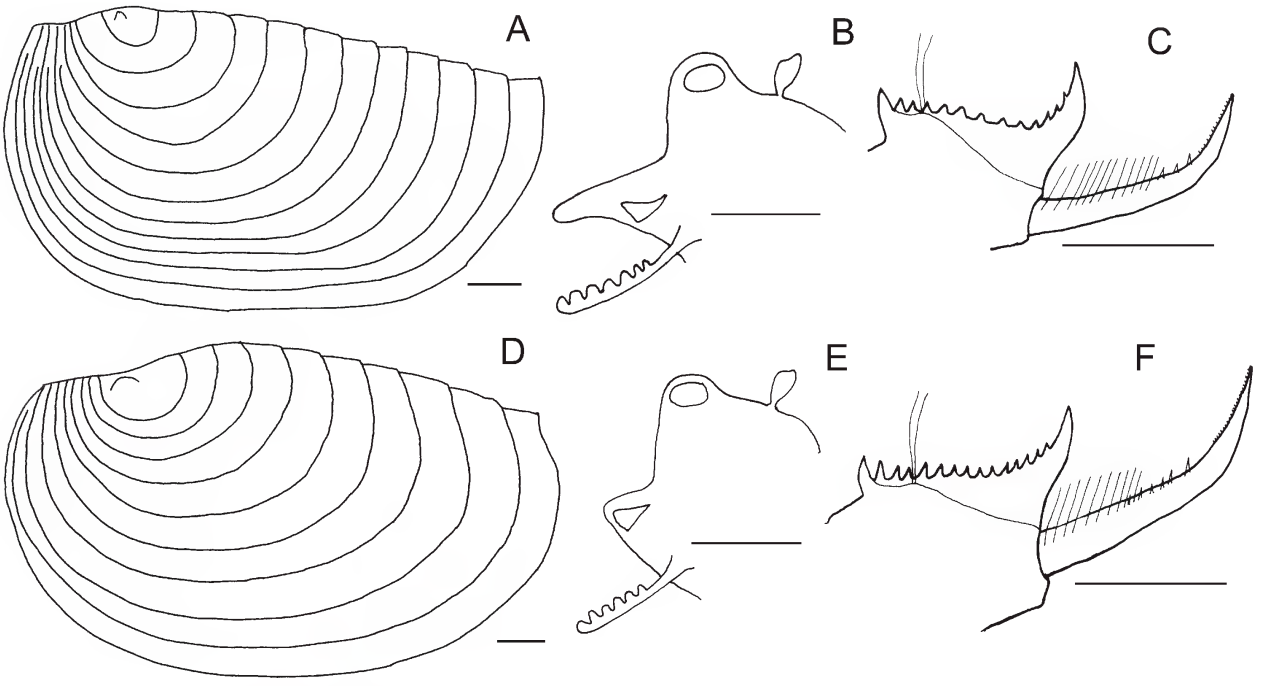

Fig. 12. *Limnadopsis occidentalis* n.sp., Boolathana Station, via Carnarvon, WA. Male: (*A*) carapace; (*B*) head; (*C*) telson. Female: (*D*) carapace; (*E*) head; (*F*) telson. For clarity some growth lines of the carapace are incompletely shown anterior to umbo. Scale bars 1 mm.

lindrical to muffin-shaped in *L. parvispinus* with multiple parallel grooves in the outer cortex; (*d*) most flagellomeres have six dorsal spines in *L. parvispinus*, but five in *L. occidentalis*; (*e*) fewer setae and fewer spines on the caudal claws in *L. occidentalis* (ca 12 setae in *L. occidentalis* and c. 15 in *L. parvispinus*; 2–6 spines in *L. occidentalis* and 4–9 spines in *L. parvispinus*); and (*f*) usually one fewer lobule in the first antenna in *L. occidentalis* (6–9, verses 7–10 in *L. parvispinus*).

Limnadopsis paradoxa n.sp.

Figs. 2G, 4D, 5K,L, 13

Types. Holotype ♂ WAM C39341, allotype ♀ WAM C39342, paratypes 2♂, 2♀, WAM C39343, 3♂, 2♀, AM P76808. Type locality: Western Australia, E of Grass Patch, Sieda Farm, Fitzgerald Paddock 81, temporary pool, 33°13'S 121°47'E, 2.ii.2007, B.V. Timms.

Other material. **Western Australia**: 4♂, S of Newdegate, Lake Bryde, 33°21'S 118°49'E, 21.iii.2006, D. Cale, WAM C39344; c. 20 individuals, S of Newdegate, Lake Bryde East, 33°22'S 118°54'E, 21.iii.2006, D. Cale, WAM C39345; c. 20 individuals, SE of Salmon Gums, along Guest Rd, temporary pool in paddock, 33°06'S 121°46'E, 25.i.2007, B.V. Timms, WAM C39346; > 50 individuals, E of Grass Patch, Sieda Farm, Fitzgerald Paddock 81, temporary pool, 33°13'S 121°47'E, 2.ii.2007, B.V. Timms, WAM C39347; >50 individuals, SE of Scaddan, Truslove Nature Reserve, a paperbark swamp, 33°20'50"S 121°46'5"E, 27.i.2007, B.V. Timms, WAM C39348. **South Australia**: 1♂, N of Woomera, Olympic Dam, 30°28'S 136°44'E, 12.ii.1981, M.J. Tyler, SAM C6351. **New South Wales**: 1♂, near Wilcannia, roadside ditch 19.5 km east of town, 31°41'S 143°427'E, 14.i.2007, B.V. Timms.

Habitat and distribution. *Limnadopsis paradoxa* lives in freshwater intermittent ponds and lakes, that are somewhat turbid or humic. More is known about the habitat of this new species than the others, because the author is personally familiar with the area. The ponds and lakes fill every few years and may take two or more years to dry (e.g., Lake Bryde, Cale *et al*., 2004) or dry within months (e.g., pools on Sieda Farm, A. Longbottom, pers. comm.). In all sites it was found only in the early period of inundation. It is known mainly from the southeastern wheatbelt of Western Australia, specifically south of Newdegate and north of Esperance. Two outlier populations were found much further east, in central South Australia and in southwestern NSW.

In Lake Bryde, it was collected in March, 2006, six weeks after a major filling, and at the time the lake was fresh (EC 549 µS/cm), alkaline (pH 7.8), warm (21.8°C), well oxygenated (88% saturation), and only slightly coloured (D. Cale, pers. comm.) This lake fills to overflowing only occasionally (every few years in the 1990s to 2000s, S. Halse, pers. comm.); normally the episodic fillings result in a shallow, fresh to slightly saline lake that takes 12–24 months to dry. At such times it holds the clam shrimps *Caenestheria* sp. and *Caenestheriella* sp., but apparently not *Limnadopsis paradoxa* (Cale *et al*., 2004).

In seven sites at Grass Patch it appeared as adults within three weeks of filling in late January, 2007. These ponds are c. 20–50 m in diameter, saucer-shaped and up to 2 m deep. They were once *Melaleuca* swamps, but many are now usually farmed for cereals. They fill partially, or deeply as

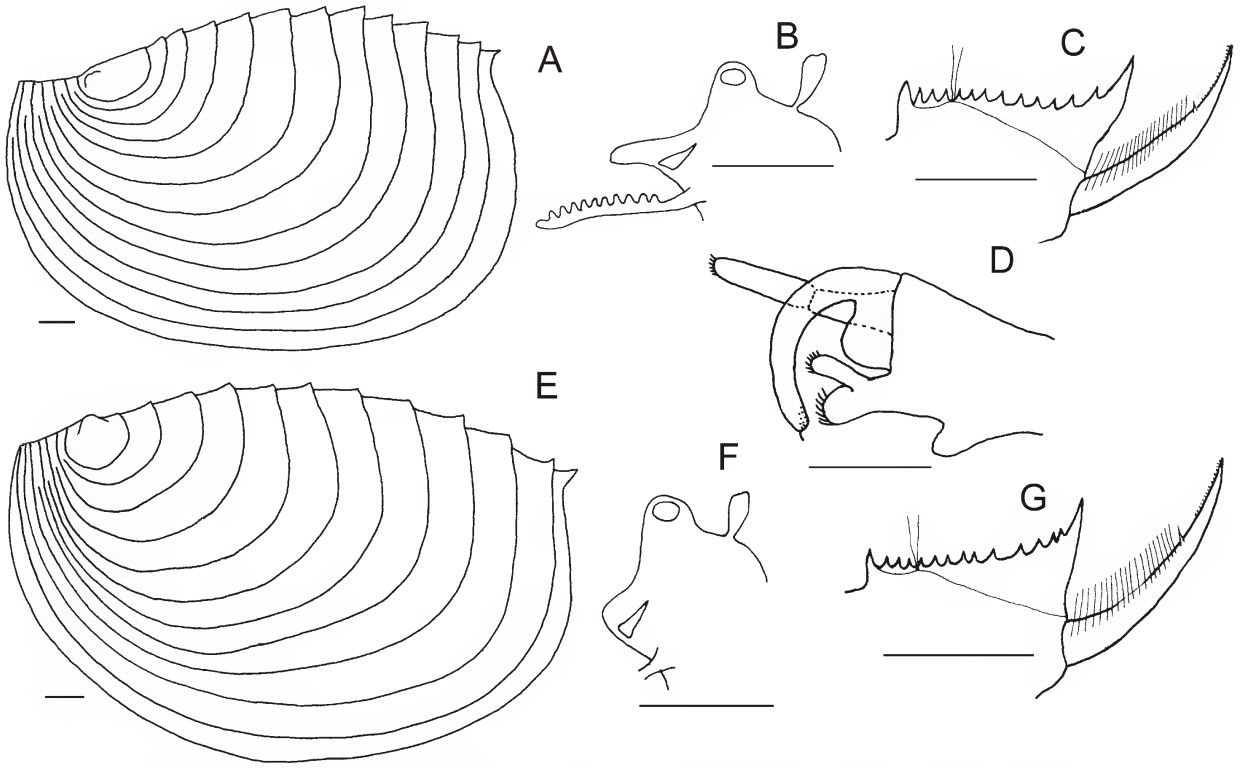

Fig. 13. *Limnadopsis paradoxa* n.sp., Sieda Farm, Grass Patch, WA. Male: (*A*) carapace; (*B*) head; (*C*) telson; (*D*) second clasper. Female: (*E*) carapace; (*F*) head; (*G*) telson. For clarity some growth lines of the carapace are incompletely shown anterior to umbo. Scale bars 1 mm.

in 2007, in wet summers, generally about once every 5–10 years (A. Longbottom, pers. comm.). Their water is humic (40–150 NTU), fresh (conductivity 260–440 µS/cm), warm (21–28°C), and acid to slightly alkaline (pH 5.8–7.4). By early March 2007, all of the ponds sampled had declining senescent populations, or none at all.

Etymology. The species name derives from the paradox presented upon first examination: it has a carapace resembling *L. birchii* and a body-form superficially resembling *L. tatei*, but it differs from these two species on detailed examination.

Male. Carapace (Fig. 13A) 14.6 mm long by 9.9 mm deep, L:D ratio c. 1.5. Dorsal margin doubly curved so lowest point at anterior umbo area and highest point about two-thirds of way along the hinge line. Hinge line uneven with growth lines protruding as small carinae, these generally more prominent posteriorly. Umbo humped dorsoanteriorly. Growth lines 12, expressed, crowded anteriorly, but more spaced spaced posteriorly. Carapace coloured dark humic brown.

Head (Fig. 13B) with a pear-shaped pyriform frontal organ posteriorly, preceded by rounded prominence containing eye, then by large rostrum at right angles to head. Length of rostrum similar to length of anterior surface of head and about twice its own basal width. Rostrum curved downwards apically and containing triangular naupliar eye dipping at angle to rostrum axis and occupying much of its basal area.

First antenna with 11 subequal lobes, slightly longer than peduncle of second antenna. Two flagella each bearing 15–18 beaded flagellomeres, each of latter with up to 6–7 spines evenly spaced along dorsal surface.

Trunk segments 26. Dorsally, posteriormost segment with spineless protuberance, preceding 7–8 segments each with 3–5 spines on protuberance, then further anteriorly another 7 segments with 5–9 long setae each. Hand of claspers with blunt narrow outgrowth near inner basal corner. Third thoracopod (Fig. 4D) similar in structure to that of *L. birchii*. Proportions of endites, endopod, exopod and epipodite slightly different, and significantly palp of fifth endite slightly shorter than fifth endite and epipodite proportionally smaller. Other thoracopods of same basic structure, but without palp and with larger epipodite.

Telson (Fig. 13C) with two rows of 13 to 14 strong, subequal spines, although the first spine slightly larger than next few spines and curving slightly posteriorly, middle spines slightly smaller and posterior spines more widely spaced, and sharper last spine near apex of claw. Two telsonic setae inserted on protuberance about one quarter of way along dorsal side of telson. Caudal claws well developed, at least twice as large as telsonic claws, curved concavely dorsally, with basal two-thirds bearing about 20 setae mesodorsally and terminating in a spine. Apical third of claw with many fine denticles dorsally.

Female. Carapace (Fig. 13E) 13.5 mm by 9.7 mm. Similar to that of male, but anterior concavity less pronounced and highest point of carapace at about midlength. Carinae of growthlines prominent, but blunt compared with those of male.

Head (Fig. 13F) similar to that of male, but rostrum short, about as long as deep, and blunt. Naupliar eye of about same size and position as in male, thus occupying much of rostrum. First antenna shorter than in male, with about 8 lobes. Second antenna as in male.

Number of body segments, and details of telson (Fig. 13G) similar to those in male.

Eggs (Figs. 4L,M) top-shaped, with prominences dorsal and ventral and about 5 prominences around equator. Typically about 16 grooves between equator and dorsal and ventral prominences, and about 3–4 grooves between each equatorial prominence. Ridges between grooves may be straightish or Y-shaped, the latter generally in the fields between equatorial and dorsal or ventral grooves. Sometimes only 4 equatorial prominences present and grooves somewhat randomly distributed. Maximum dimensions about 250 µm (range 241–254 µm, n = 20).

Variability. The carapace size varies from c. 13 to16 mm, growth lines from 10 to 14, first antennal lobes 9 to 11, telsonic spines 15 to 18, and caudal claw setae from 16 to 21. There is no significant variation in the characteristic carapace shape, and all specimens have just one spine on the caudal claws.

Comments. *Limnadopsis paradoxa* resembles small specimens of *L. birchii*, on account of its size, general shape, development of the carinae, and perhaps colouration. However, the body inside bears absolutely no resemblance to that of *L. birchii*. For instance there are 26 body segments, not 32, and there are only c. 14 telsonic spines on a almost straight edge compared to c. 50 spines on a doubly curved edge. The new species is most like *L. tatei* but has more growth lines, more lobes on the first antenna, more telsonic spines and more setae on the caudal claws. Perhaps it could be regarded as a bigger form of *L. tatei*, but the shape of the carapace is distinctive, particularly the concave dorsal surface and the lateral development of the umbo. The smaller first:second telsonic spine size ratio in *L. paradoxa*, and more numerous caudal claw setae are also distinctive. *Limnadopsis pilbarensis* n.sp. (see below) differs by having a convex edge in the umbo area, much less pronounced development of the dorsal outgrowths of the growth lines, and fewer telsonic denticles and setae on the caudal claws.

The eggs of *L. paradoxa* and the three other above-mentioned species are distinctive among themselves. At 40× magnification, eggs of *L. birchii* and *L. tatei* are smoothly round with groups of parallel grooves, more of the latter in *L. birchii* than in *L. tatei*. Eggs of *L. paradoxa* and *L. pilbarensis* both have rough surfaces, but those of *L. pilbarensis* have many (> 20) spines and those of *L. paradoxa* have just a few (<8) rounded prominences. These distinctions are even more pronounced as observed by SEM (Fig. 4).

Limnadopsis pilbarensis n.sp.

Figs. 1, 2H, 5F, 14

Types. Holotype WAM C39349, allotype WAM C39350, paratypes 1♂, 1♀, WAM C39351. Type locality: Western Australia, Pilbara, N of Karratha, Burrup Peninsula, unnamed rockhole, 20°34'25"S 116°48'27"E, A Pinder & J. McRae, 20.viii.2005.

Other material. **Western Australia**: 8 individuals, Pilbara, Chichester Range, Beabea Creek, 21°36'S & 118°38'E, J. Wombey, 21.vi.1970, WAM C38103; 1 ♂, 3♀, via Paraburdoo, Ratty Spring on Pirraburdu Creek 7 km west of Paraburdoo, 23°15'S 117°28'E, 1.iv.1979, J.A. McNamara, WAM C39352; 6 individuals, Glen Ross Creek, Pilbara, WA, 24°10'44"S 118°01'48"E, site PSW085 of Department of Environment and Conservation, collected by A. Pinder & J. McRae, 9.ix.2005.

Etymology. This species gains its name from the district, the Pilbara, from which all the present material was collected. I also wish it to honour my great-uncle, Tom Starr, who spent much time "in the early days" exploring for gold in the Pilbara and made a significant discovery at Marble Bar in the 1930s.

Male. Carapace (Fig. 14A) 10 mm long by 6.5 mm deep, L:D ratio c. 1.5. Dorsal margin curved with highest point just posterior to larval valve growth line, i.e. about one-third of way from anterior end; curvature greater anteriorly than posteriorly to this high point. Growth lines 9–10, expressed, crowded anteriorly, spaced posteriorly. Posteriorly at hinge line, younger (i.e. outer) growth lines humped, each more so than previous line. Carapace with granular surface texture.

Head (Fig. 14B) posteriorly with pyriform frontal organ posteriorly, preceded by rounded prominence containing eye, a tiny protuberance below eye and a large rostrum at right angles to head. Rostrum somewhat longer than distance between eye and pyriform organ, curved downwards at its apex, and containing triangular naupliar eye dipping at angle to the rostrum axis and occupying much of its basal area. Rostrum length twice its own basal width.

First antenna with 9–10 fairly evenly-sized lobes; usually a spine present near base on same side as lobes. Second antenna with two flagella each of about 12–16 beaded flagellomeres, these of variable length but generally longer and bigger basally. Flagellomeres around midlength each with 7–9 setae on dorsal surface.

Trunk segments 25–26 in number. Dorsally, posteriormost segment with spineless protuberance, preceding 7–8 segments each with 3–5 spines on protuberance, then further anteriorly another 7–8 segments with long setae varying from many posteriorly to 1–2 on more anterior segments. Hand of claspers (Fig. 14D) with asymmetrical outgrowth near inner basal corner. Immovable finger with numerous spines apically, central ones short and stout, giving way to long, thin curved spines on inner edge. Palp of movable finger short with setae apically. Base of movable finger with evenly curved, slight protuberance opposite immovable finger, and evenly curved finger terminating in small spine. Palp of hand two-segmented, as long as hand in first clasper and about half as long again in second clasper; distal segment bearing many short setae apically, but no setae on junction of palp's two segments.

Telson (Fig. 14C) armed with two rows of about 11 strong, subequal spines, although anterior spine almost twice as

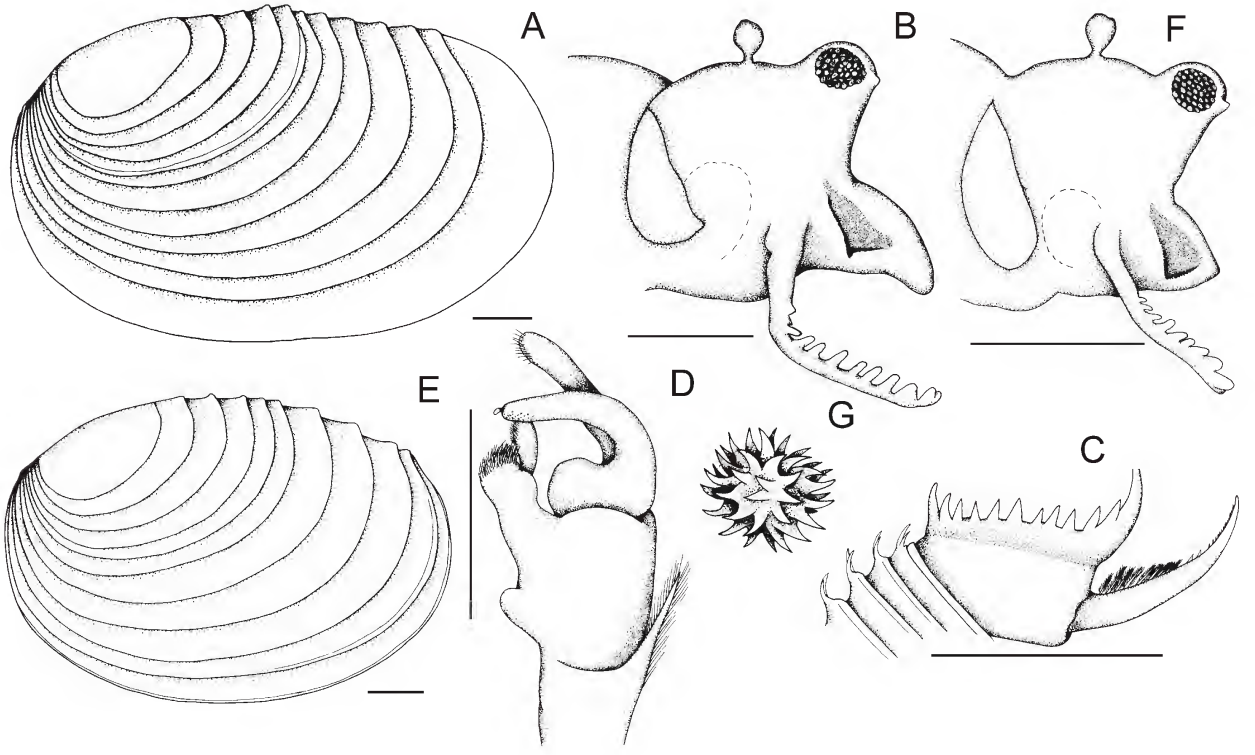

Fig. 14. *Limnadopsis pilbarensis* n.sp., unnamed rockhole, Burrup Peninsula, Pilbara, WA. Male: (*A*) carapace; (*B*) head; (*C*) telson; (*D*) first clasper. Female: (*E*) carapace; (*F*) head; (*G*) egg. Scale bars 1 mm. Drawn by Jane McRae.

large as the others and curving slightly posteriorly; last 2–3 spines on curved, telsonic claw; this claw curved anteriorly and more than twice as long as basal width.Two telsonic setae inserted on protuberance about one quarter the way along dorsal surface of telson. Caudal claws well developed, at least twice as large as telsonic claw and curved concavely forward. Basal half thick, almost straight, and bearing about 10 shortish setae mesodorsally. Two short spines located about two thirds of way along each caudal claw on dorsal surface, followed by row of many denticles situated dorsally on pointed apex of caudal claw.

Female. Carapace (Fig. 14E) 10 mm by 6 mm. Similar to that of male, but hinge line slightly more curved.

Head (Fig. 14F) similar to that of male, but rostrum short, about as long as deep, and blunt. Naupliar eye of about same size and position as in male, occupying much of rostrum. First antennae shorter than in male, with about 6 unequal lobes and generally no basal spine. Second antenna as in male, but generally with only about 12 beaded flagellomeres, rarely a few more to a miximum of 15.

Number of body segments, posterodorsal armature, and telson similar to those in male.

Eggs (Figs. 5F, 14G) subspherical, about 250 μm in diameter (range 247–252 μm, n = 5). Surface very irregular with deep conical pits (n = c. 20) bordered by thin, expressed ridges. Where three ridges meet, surface is further expressed as spines visible in light microscopy.

Comments. *Limnadopsis pilbarensis* is most similar to *L. tatei*. Many features of *L. pilbarensis* lie within the range of variability seen in *L. tatei*, including valve size, number of growth lines, rostrum shape and relative size, first antenna lobe number, number of flagellomeres of second antenna, number of body segments, gross structure of claspers, and many features of the telson. However *L. pilbarensis* is distinctive in its carapace structure: (*a*) it lacks dorsal carinae, although the dorsal margin is humped where the growth lines meet it, (*b*) in males the dorsal margin is always markedly curved whereas in *L. tatei* it is weakly curved or straight, (*c*) carapace tends to be ballooned in *L. pilbarensis* but *flattish* in *L. tatei*, and (*d*) the growth lines in *L. pilbarensis* are particularly clearly visible, being well expressed and generally coloured brown to black on a yellowish carapace background. The dorsal telsonic spines are also different in the two species: although there are similar in number, those in *L pilbarensis* are subequal and fairly evenly spaced, while in *L. tatei* they vary much in size and spacing. Also, the anteriormost spine is about 1.5 times the size of the others in *L. pilbarensis* and 2 times or greater in *L. tatei*.

Limandopsis pilbarensis cannot be confused with the other species of *Limnadopsis* besides *L. tatei*. It is easily distinguished from *L. birchii* by the much smaller size, fewer body segments, significantly fewer telsonic spines and lack of carinae on the carapace. Though similarly lacking carapace carinae, *L. parvispinus* is a little larger (> 12 mm) and significantly has more (>13) telsonic spines and more (>11) growth lines than *L. pilbarensis*. Furthermore, the carapace in *L. parvispinus* is expanded posteriorly beyond the dorsoposterior corner, but not in *L. pilbarensis*. Among limnadiids and possibly most Australian branchiopods, the eggs are particularly distinctive with their conical pits and spinous outgrowths.

Limnadopsis brunneus Spencer & Hall, 1896, nomen dubium

Limnadopsis brunneus Spencer & Hall, 1896: 243, pl. 23, figs. 28–29; Sayce, 1903: 250; Wolf, 1911: 254 (list); Dakin, 1914: 295 (list); Henry, 1924: 122 (list), 132 (key); Brtek, 1997: 58 (list).

Limnadiopsis brunneus.—Daday, 1925: 183–184, fig. 124 (misspelling of genus name); Schneider & Sissom, 1982: 72–73 (misspelling of genus name).

Types. None designated, though the four dried specimens used to erect this species (Spencer & Hall 1896) would be syntypes, but they are missing. Type locality: Knuckeys Lagoon, Darwin, NT.

Comments. Spencer & Hall (1896) erected this species, noting only that the carapace carinae were not as strongly developed as in *L. tatei*, and that there were 30–34 growth lines. Their diagram shows only 20 growth lines, and virtually no dorsal carinae. Immediately this presents a major problem, as the diagram and brief description do not match. No specimens are available in any Australian Museum, although Schneider & Sissom (1982) claimed to have found this species in the Kimberley. These specimens are now lost (S. Sissom, pers. comm.) and there is doubt over their identity based on their description of only 20 growth lines (see Richter & Timms, 2005). The author visited the type locality in the wet season (late February, 2007) and was unable to find any specimens, nor later raise any *Limnadopsis* from dried mud collected from the site. As a further complication, it is just possible the presently described *L. multilineata* is in fact *L. brunneus*, based on the written description of the latter. Similarly, and based only on Spencer & Hall's (1896) diagram, the present *L. minuta* could be in fact *L. brunneus*. Hence the animal remains an enigma and therefore is considered a nomen dubium.

Discussion

Variability. Spinicaudatans are notoriously variable in their morphological characteristics (D.C. Rogers, pers. comm.). Straškraba (1965a) noted that in the Limnadiidae, and specifically in *Limnadia lenticularis*, the carapace shape, number of growth lines, dorsal extension of the growth lines, and numbers of telsonic spines and setae and spines on the caudal claw are all variable in expression. Cycizids are even more variable in these and other characters (Straškraba, 1965b). The situation in *Limnadopsis* is no exception, with variation within and between populations noted particularly in the numbers of growth lines, telsonic spines, and spines of the cercopods, and to a lesser extent in carapace shape, and expression of dorsal carinae of the carapace. Adult size is also variable, but this is also influenced in spinicaudatans by nutrition during development (D.C. Rogers, pers. comm.). Although the dorsal trunk spination and setation has been described for each species, these features are also variable within species, probably at least partly associated with predation pressure (D.C. Rogers, pers. comm.). Some species are more variable than others, with *L. tatei* being the most variable, and *L. birchii* the least variable, of those for which numerous specimens have been examined.

Sex is easily determined by examining the rostrum (long in males and short in females) and by the presence of claspers in males. Carapace shape can also be different, especially in *L. tatei* and *L. multilineata*, and to a much lesser extent in *L. parvispinus, L. paradoxa*, and *L. pilbarensis*, with carapaces being more humped dorsally in females than in males of these species. An interesting intersex condition was observed in one population of *L. parvispinus*, in which males had a short rostrum and claspers smaller than usual. Of various intersex conditions known in limnadiids this is most unusual (Sassaman, 1995; S. Weeks pers. comm.).

Despite this variability, by reference to many characteristics, species can be delineated, despite overlap in some counts such as number of growth lines or telsonic spines. More disconcerting is the occasional finding of a specimen well outside the normal range in just one character when the remaining features all indicate a particular species. This is seen mainly in counts of telsonic spines, so that ranges given for some species, e.g., *L. tatei, L. parvispinus*, are much wider than normally seen in an attempt to encompass this variability. Perhaps such oddities are explained by development abnormalities. More easily explained are areas of the body so damaged during development that they assume a different shape or number of parts than usual. Body parts most easily damaged seem to be the male rostrum (e.g., Fig. 8B of *L. parvispinus*), carapace edge, and the caudal claws.

In diagnosing species, the most useful characters, because of their consistency between species, are shape of the carapace, particularly the convexity of the dorsal margin and posterior edge; the relative development of the dorsal carinae; the number of body segments; the number of spines on the caudal claws; and also the surface morphology of the eggs. Also useful in differentiating some species are, the number and relative size of the telsonic denticles, the curvature of the dorsal telsonic surface, the number and expression of the growth lines, the number of spines on the dorsal margin of the middle flagellomeres of the second antennae, and the number of caudal claw setae. There is little difference between species in the macroscopic structure of the claspers, although microscopic studies using SEM is proving fruitful in *Limnadopsis* (S. Richter, pers. comm.). From the study of the thoracopods of just four of the eight species, there seems to be only minor differences between species, although all are clearly different from those of other spinicaudatan genera. Thoracopods of *Limnadopsis* (Fig. 4) are characterized by a long fifth endite, that is of similar structure to the endopod, and by a one-segmented palp on just the third pair of thoracopods, and in males only. The structure of the head, second antenna and to a lesser extent the first antennae are conservative throughout the genus and of little use in delineating species.

Limnadiopsium. Novojilov (1958) split the genus *Limnadopsis* (misspelt as *Limnadiopsis*) into *Limnadiopsis* (sic) and *Limnadiopsium*. Novojilov placed *Limnadopsis tatei* into his *Limnadiopsium* and left *Limnadopsis birchii* (misspelt as *L. brichii*) in *Limnadopsis*. He was apparently unaware of *Limnadopsis parvispinus* and thought *L. brunneus* belonged to a third genus. Furthermore, he erected holotypes "on paper" for both species based on the material the original authors used in their descriptions (for *L. birchii*: "Holotype: spécimen décrit par Baird"; for *L. tatei*: "Holotype: spécimen décrit par Spencer et Hall 1896"—Novojilov, 1958:104–105) It seems from the text that Novojilov (1958) did not see the original descriptions as he quotes Daday de Deés, 1925, fig. 122 in the case of *L. birchii* and fig. 123 in the case of *L. tatei*. No type material was designated for these two species by their authors and indeed for *L. birchii* and *L. brunneus* no type specimens of any designation exist (Timms, 2006). For *L. tatei* it is only now that a neotype has been chosen (see earlier). The misspelling of just about every name used, the erection of invalid holotypes and the omission of the other known species of *Limnadopsis*, is enough to cast doubt on this work.

Novojilov (1958) claimed *Limnadiopsium* to be distinct from *Limnadopsis* by reason of the smaller number of appendages, presumably meaning 26 as against 32 in *L. birchii*; spines on the telson being of various dimensions compared with uniform spines in *L. birchii*; the straight dorsal edge of the carapace in *Limnadiopsium*, presumably in contrast to the convex edge in *Limnadopsis*, and the "spines" (= carinae) on the dorsal edge of the carapace being present in all stages of development in *Limnadiopsium* but only in the last stages in *L. birchii*. Detailed studies show that all these claims are spurious. The extent of development of the carinae varies between populations, so that on this character alone, some *L. tatei* and *L. birchii* populations would be excluded from both *Limnadopsis* and *Limnadiopsium* because of not having carinae even as adults. Also, some populations of *L. tatei* do not have a straight dorsal edge to the carapace, so would be excluded, and no female *L. tatei* has a carapace with a straight dorsal edge. As for the telsonic spines, while there is a contrast between *L. tatei* and *L. birchii*, other species show intermediate conditions. Finally, five other species of *Limnadopsis* have 26 trunk segments (25 in some specimens), and *L. minuta* has 24, so that on this character they should be aligned with *L. tatei*, not *L. birchii*. As shown above they are all otherwise distinct from *L. tatei*. In summary, *L. tatei* is not distinctive enough to warrant removal into its own genus *Limnadiopsium*, so Novojilov's (1958) work is rejected.

Biogeography. Two species of *Limnadopsis* (*L. birchii* and *L. tatei*) are widespread in the drier parts of Australia, showing no consistent differences across this broad range. Eastern Australia is populated by just one local species, *L. parvispinus* but in the west and northwest there are five localized species with somewhat different latitudinal distributions (cf. anostracans in Western Australia: Timms, 2002, 2008). Southern Western Australia has *L. paradoxa*, the mid north and northwest has *L. occidentalis*, the northwest has *L. pilbarensis*, and the far north has *L. minuta* and *L. multilineata*. The inland of Western Australia has *L. birchii* and *L. tatei*. Clouding this picture is the presence of isolated populations of the southern Western Australian species *L. paradoxa* in central South Australia and in western New South Wales; perhaps it is spreading to the east from its base in southern Western Australia. The higher diversity of *Limnadopsis* in the west is typical of many organisms of inland waters in Western Australia (e.g., charophytes, A. Garcia, pers. comm.; anostracans, Timms, 2002, 2004, 2008; mytilicyprinid ostracods, Halse and McRae, 2004; many cladocerans, Hebert & Wilson 2000, R. Shiel, pers. comm.). Despite this diversity in Western Australia, no congeneric occurrences have been noted, unlike in the Paroo of the eastern inland, where *L. birchii* and *L. parvispinus* often co-occur (Timms & Richter, 2002).

Key to species

In using this key, it is necessary to be aware of the variability between individuals and populations of the same species. Comparative features in the couplets are arranged so the most reliable are given first, and the least reliable last. While almost all specimens will fit all key features of a given species, occasionally individuals or populations will be aberrant and disagree with one feature, usually the last. In such cases identification should be confirmed using the additional characters given for each species in square brackets.

1 Telson with c. 50 dorsal spines in each row; 32 body segments; most antennal segments with >12 spines ..... *L. birchii* Spencer & Hall

[Also: mature specimens large, generally >18 mm long and up to 30 mm; L:D ratio c. 1.5; 14–16 growth lines; dorsal carinae of growth lines reach forward to proceding growth zone; dorsal surface of telson double-curved in a sinewave; caudal claws evenly curved and with >10 dorsal spines at midlength; carapace with dorsoposterior corner sharp, composed of a protruding growth line carina; eggs round with parallel grooves; carapace usually translucent yellow-brown.]

—— Telson with < 25 dorsal spines in each row; 24–26 body segments; most antennal segments with <10 spines 2

2 Dorsal margin of carapace with irregular, asymmetrical growth line carinae; carapace with robust growth lines; caudal claws with <3 dorsal spines at midlength 3

—— Dorsal margin smooth, or almost so with only very minor steps at each growth line-dorsal margin junction; carapace usually, but not always, with indistinct growth lines; caudal claws with usually >4 dorsal spines at midlength 5

3 Posterior edge of carapace not, or just barely expanded beyond dorsoposterior corner, latter usually bearing a prominent spine; anteriormost dorsal telsonic spine 1.5–2 times size of next few spines; carapace hinge line of male straight or almost so ..... *L. tatei* Spencer & Hall

[Also: mature specimens small, usually <10 mm; L:D ratio c. 1.6; 7–11 (usually <9) growth lines; growth line carinae barely extending into preceding growth zone; these carinae variously developed, sometimes hardly developed at all; 5–7 spines on middle second antennal flagellomeres, all arranged linearly; dorsal surface of telson straight or evenly and slightly concavely curved and bearing two rows of 9–13 (usually c. 12) spines, these sometimes unevenly sized and spaced; caudal claws with straight basal section bearing >12 (rarely as few as 8) proximal setae and <3 dorsal spines at midlength; eggs round with grooves parallel only for short distances; carapace usually translucent yellow-brown.]

—— Posterior edge of carapace expanded into wide curve protruding beyond the dorsoposterior corner, latter bearing a weak spine, if any at all; anteriormost dorsal telsonic spine <1.5 times as large as the next few spines; carapace hinge line markedly curved, even in males 4

4 Dorsal hinge line of carapace in umbo area convexly curved; telson with 12–14 spines evenly spaced; anteriormost telsonic spine c. 1.5 times as large as next few spines ..... *L. pilbarensis* n.sp.

[Also: mature specimens c. 10 mm long with 9–11 growth lines; L:D ratio c. 1.5; dorsal margin of carapace stepped, and with hardly any carinal outgrowths; up to 9 spines on middle flagellomeres of second antenna, all arranged linearly; caudal claw with straight basal section bearing c. 10 proximal setae and <3 (rarely more) dorsal spines at midlength; dorsoposterior corner of carapace blunt with projection at the end of the growth line; eggs round with many (>12) narrow, sharp spikes, pitted between these spikes; carapace yellow with very distinct dark growth lines.]

—— Dorsal hinge line of carapace in umbo area concavely curved, i.e. depressed; telson with 14–18 spines unevenly spaced; anteriormost telsonic spine slightly bigger than next few spines ..... *L. paradoxa* n.sp.

[Also: mature specimens c. 13–15 mm long with 12–13 growth lines; L:D ratio c. 1.5; dorsal margin of carapace markedly stepped or with small carinae at each growth line-dorsal hinge line junction; middle flagellomeres of each second antenna with 6–7 spines on anterior margin, all arranged linearly; caudal claws evenly curved with c. 18 proximal setae and usually just one spine at midlength; dorsoposterior corner of carapace sharp due to a spine-like outgrowth of growth line there; eggs top-shaped (a prominence dorsally and ventrally, and 4–5 equatorially); carapace coloured dark humic brown.]

5 Growth lines in mature specimens >20, often up to c. 30; carapace with a distinct but blunt dorsoposterior corner and with a much expanded posterior/ventroposterior edge; dorsal margin of male carapace almost straight ..... *L. multilineata* n.sp.

[Also: umbo expressed and pointed; L:D ratio c. 1.6; growth lines usually crowded at margin, though this could be due to ecological conditions; height of eye generally less than that of pyriform organ; first antennal lobes c. 6–7; about 18–20 flagellomeres on second antenna, middle ones with 3–5 spines arranged linearly; dorsal telsonic spines 13–18, first spine a little (<1.5) bigger than remainder; caudal claws with c. 15 setae, last few intermixed with c. 5–6 caudal claw spines; eggs bell-shaped; carapace coloured lustrous dark brown.]

—— Growth lines <19; carapace without protruding dorsoposterior corner and posterior edge may be widened but not in ventroposterior area; dorsal margin of male carapace convexly curved 6

6 24 trunk segments; telson with spiniform process on ventroposterior corner below cercopod; 18 growth lines ..... *L. minuta* n.sp.

[Also: carapace <10 mm long; no sexual dimorphism in carapace shape; L:D ratio c. 1.9; lobes on first antenna c. 8 in males and c. 6 in females; flagellomeres of second antenna numbering about 18–20 and middle flagellomeres with c. 4 spines each with 2–3 of these crowded apically, leaving basal anterior surface of segment bare; c. 17 telsonic spines in each row; 12–15 caudal setae, 3–5 caudal spines, posteriormost 3 times larger than others; dorsal surface of telson between spine rows with a marked depression immediately posterior to the insertion mound of telsonic setae; eggs polyhedral.]

—— 25–26 trunk segments; telson without spiniform process on ventroposterior corner.; <17 growth lines 7

7 Dorsal telsonic spines 18–24; cercopods with 4–9 spines at midlength; dorsal telsonic spines evenly sized and spaced ..... *L. parvispinus* Henry

[Also: carapace up to 16 mm in length, L:D ratio c. 1.7; first telsonic spine usually about 1.5 times the next few; middle antennal segments with 4–7 spines each, with perhaps not all linearly arranged; c. 15 setae on caudal claws; 25–26 body segments; dorsal hinge of carapace not depressed at or near umbo; eggs subconical cylinders; carapace of various colours, often variegated brown.]

—— Dorsal telsonic spines c. 13–16; cercopods with 3–5 spines midlength; telsonic spines variable in size and spaci ..... *L. occidentalis* n.sp.

[Also: carapace up to about 12mm in length, L:D ratio c. 1.6; the first telsonic spine variable in size with respect to the others; middle flagellomeres of second antenna with 5–7 spines each, not all arranged linearly; 12–15 setae on caudal claws; 25 body segments; dorsal margin of carapace often depressed at umbo and anterior to it; eggs round with short randomly orientated grooves; carapace various colours often yellowish.]

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Two New Species of *Gnathothlibus* Wallengren from Fiji and Samoa and a New Species of *Theretra* Hübner from New Guinea (Lepidoptera: Sphingidae)

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ABSTRACT. Two new species of hawk moths from Fiji and Samoa, respectively *Gnathothlibus fijiensis* n.sp., and *G. samoaensis* n.sp., are described and figured, and distinguished from *G. vanuatuensis* Lachlan & Moulds, *G. saccoi* Lachlan & Moulds and *G. eras* (Boisduval). A new species of *Theretra, T. tabubilensis* n.sp. from Papua New Guinea is described and figured. The new species is distinguished from the sympatric *T. indistincta papuensis* Joicey & Talbot and *Theretra clotho celata* (Butler), and the lectotype of *T. i. papuensis* is designated.

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Three species of *Gnathothlibus* Wallengren, 1858 have been described from the southwestern Pacific region. *Gnathothlibus eras* (Boisduval, 1832) is reported, as a subspecies of *G. erotus* (Cramer, 1777), to occur from the Australian Region to Tahiti (D'Abrera, 1987), *G. saccoi* Lachlan & Moulds, 2001 [= *G. malleti* Schmit, 2002 (Schmit, 2003)] and *G. vanuatuensis* Lachlan & Moulds, 2003 are known only from Vanuatu (Lachlan & Moulds, 2001, 2003; Schmit, 2002).

Two undescribed species of *Gnathothlibus*, both closely resembling *G. eras*, and both previously confused with it, have been collected. One was collected in Fiji on the main island of Viti Levu in April, 2008, the other was collected on the island of Upolu, Samoa, in November, 2008. They are described in the present work.

In the early 1990's the author also collected a large series of males and females of another sphingid genus *Theretra* Hübner, [1819], from the Tabubil area of the Western Province, Papua New Guinea. This collection could readily be classified into two species *Theretra indistincta* (Butler, 1877) and a closely related but undescribed species. The two taxa are consistently distinct, no evidence of morphological intergradation was found despite several years of sampling and examination of large numbers of specimens. Evidently, sympatry has not resulted in hybridization.

Bibliographic information and notes on the generic diagnoses of *Gnathothlibus* and *Theretra* are given by D'Abrera (1987).

Materials and methods

All specimens sampled at the various localities were collected using mercury vapour lights run from sunset to just before sunrise. The specimens were then deep frozen before being set for examination. All measurements are given in millimetres. This study was based on extensive material in the author's private collection, (RBLC), and material in the Australian Museum, Sydney, (AM). Some specimens have been deposited in the Natural History Museum, London, (BMNH). Wing venation is that used by D'Abrera (1987). Morphological terminology used in this paper is based on that used by Kitching & Cadiou (2000).

Taxonomy

Genus *Gnathothlibus* Wallengren, 1858

Type species: *Gnathothlibus erotoides* Wallengren, 1858.

Gnathothlibus fijiensis n.sp.

Figs 1–4, 14

Type material. HOLOTYPE ♂, FIJI: 3 km E of Komave, south coast of Viti Levu, 18°13'36.2"S 177°46'25.7"E, 16 April 2008, R.B. Lachlan, AM K266025. PARATYPES 9♂♂, 2♀♀: 7♂♂ with same data as holotype but 2 dated 8 April 2008 in RBLC, 1 (AM K266026) dated 9 April 2008, 1 dated 13 April 2008, 1 dated 15 April 2008, 1 dated 16 April 2008 and 1 dated 7 December 2008 in RBLC. 2♂♂ H. Phillips, Vunidawa, Fiji, 18.8.1932, Lautoka, Fiji, 19.6.27, H. Phillips in AM. 2♀♀ with same data as holotype, 1 dated 16 April 2008 in RBLC, 1 (AM K266027) dated 6 December 2008 in AM.

Diagnosis. In male, olive green ground colour on forewings. Ventral surface of head, thorax and abdomen olive green. Mauve lateral stripe on the outer edges of the tegulae above both wings. A prominent dark, mostly straight, post median line runs from costa, where it is curved slightly distally, to inner margin. Female forewings brown with prominent dark, mostly straight, post median line as in male. Genitalia with uncus, in lateral view, long, slender, parallel-sided for nearly the whole of its length, slightly arched with the distal margin slightly convex and slightly angled backwards dorsally with a small dorsal crest. The distal margin has a small, dark ventral tooth.

Description. Male. (Figs 1,2,14). Antennae creamy-brown above, dark brown below; palpi olive green above, contrasting off white below; dorsal surface of head and prothorax darker olive green, remainder of thorax and abdomen uniform olive green; small dark median spot with posterolateral orange-brown on prothorax; thin lateral creamy-olive stripe from base of antennae to forewing, continuing as mauve on the outer edges of the tegulae above both wings. Thorax ventrally with creamy, light brown patch immediately posterior to palpi, remainder of median band creamy-olive along thorax dissipating as it reaches upper abdominal segments. Abdominal segments laterally each with orange-brown posterior margin contrasting with olive green ground colour, abdomen with four small lateral black spots surrounded clearly by white. Fore-tibae covered in long creamy-olive hair scales; proximal three segments of fore-tarsi covered in shorter creamy-olive hair scales, shortest on distal segment, longest on proximal segment.

Forewing upperside as in Fig. 1. Forewing length 38–41 mm, mean 39.6 mm (n = 7). Ground colour olive green (brighter in fresh specimens) with darker markings; some specimens exhibit less green; small black stigma with light coloured centre at end of discal cell; irregular, oblique, submarginal dark line from costa to vein M_3, wider between veins M_2 and M_3; a prominent dark, mostly straight, post median line runs from costa, where it is curved slightly distally, to inner margin; a short, irregular, subbasal band edged on each side by dark lines and curved distally, runs from costa to the dark basal patch below vein 1A+2A. Forewing underside as in Fig. 2. Ground colour burnt orange, lighter basad with two short, antemedian orange-brown streaks near costa and one near base; distally darker brown with usually two dark, irregular, parallel post median lines from costa to vein M_1; these lines may be vestigial or well developed in some specimens.

Hindwing upperside as in Fig. 1; ground colour orange; a slightly variable dark brown terminal band from apex to tornus at least 2 mm wide, slightly thinner at apex; inner margin of band slightly irregular with brown scales along veins M_1 to M_3 for about 2 mm. Hindwing underside (Fig. 2) with ground colour light orange-brown, heavily speckled with dark brown; marginal area darker from apex to tornus; dark, mostly straight, median line, thickest at costa, curving proximad from costa to vein M_1 and usually reaching vein CuA_1 but does not touch distal edge of cell; a much less prominent, small, parallel dark post median line to vein R_s, vestigial in most specimens.

Male genitalia (Fig. 14). Uncus in lateral view, long, slender, parallel-sided for nearly the whole of its length, slightly arched, distal margin slightly convex and slightly angled backwards dorsally with small rounded dorsal crest, distal margin with, dark ventral tooth; gnathos in lateral view thin, straight, distal margin tapering to a small, slightly upturned point; in dorsal view gnathos is wide basally with slightly curved sides tapering evenly to a point; valvae dorsal margin straight proximally then slightly convex, then distally straight, distal margin rounded, ventral margin gently convex; sacculus process well developed; harpe robust, distal end smooth surfaced and spine-like, upturned; aedeagus in lateral view with distal end tapered to a bluntly rounded apex with backward directed dorsal fishhook-like barb, ventrally with a small, similar barb, a little proximad of dorsal barb.

Female (Figs 3–4). Forewing length 40–44 mm. Head and tegulae dark brown. Median area of thorax and abdomen above medium brown. Thin lateral cream stripe from base of antenna to posterior edge of tegula above hindwing, not mauve as in male. Thorax below uniform orange-brown; abdomen ventrally pale pinkish-brown with four well-developed lateral white spots with small black centres. Fore-tibae covered in short hair scales, light brown on anterior edge and cream on posterior edge; fore-tarsi without hair scales.

Forewing upperside as in Fig. 3; ground colour and pattern in shades of darkish-brown, lacking green colour of male; small dark brown stigma with light centre at end of discal cell; a prominent dark brown, almost straight, post median line runs from costa and curved slightly distally to inner margin as in male. Forewing underside as in Fig. 4; ground colour medium brown, distinctly speckled with dark brown distally; a dark brown irregular, submarginal line runs from apex to tornus; two variable dark brown parallel post median lines from costa often reaching vein CuA_2.

Hindwing upperside (Fig. 3) orange as in male, but dark brown terminal band broader, with inner margin generally quite straight and suffused with orange scales; hindwing underside (Fig. 4) ground colour same as forewing but more heavily speckled with dark brown; yellowish streak along proximal side of vein 1A+2A.

Etymology. The specific name *fijiensis* is derived from the Pacific island nation of Fiji, the only known locality for the species.

Distribution. At present *G. fijiensis* is known only from the main island of Viti Levu, Fiji.

Discussion

Gnathothlibus fijiensis is readily distinguished from *G. saccoi, G. vanuatuensis* and the sympatric *G. eras* by the distinctive olive green colour on the forewings of the male, particularly in fresh specimens. It is a brighter green than seen on the forewings of *G. saccoi* males and most males of *G. vanuatuensis*. *Gnathothlibus eras* males from Fiji do not exhibit any green colouring to this degree and usually not at all. Elsewhere in the Australian-Pacific region, they are brown. Also, the forewings of *G. fijiensis* are much less heavily patterned than *G. saccoi* and it is a much smaller species than *G. saccoi*. The oblique line on the forewing of *G. fijiensis* is clearly straighter on all specimens examined than seen on *G. eras*. The forewings of the female of *G. fijiensis* easily distinguish it from the females of *G. saccoi, G. vanuatuensis* and *G. eras* by being less heavily patterned and the prominent dark brown post median line on *G. fijiensis* is angled distad slightly more than seen on the other three species and is very clearly much straighter. This is also the case in the males of *G. fijiensis*.

The distinctive mauve lateral stripe on the outer edges of the tegulae above the wings on the males of *G. fijiensis* is not seen on the other three species; they all have creamy-white lateral stripes. The hindwing dark marginal band on male and female *G. fijiensis* is not as narrow at the apex of the hindwing as seen on *G. saccoi* and *G. vanuatuensis*. This dark brown marginal band is always much narrower overall in *G. eras*, particularly in males where it is often very thin. In *G. fijiensis* and *G. saccoi* this marginal band does not spike inwardly along vein 1A+2A as clearly as it does in *G. eras* and *G. vanuatuensis*. This situation is the same in the females of each of the four species.

The fore-tarsi of *G. fijiensis* are covered in long hair scales; in *G. vanuatuensis* they are without such hair scales. On the underside of the hindwings of both male and female *G. fijiensis* the short, dark brown median line, beginning at the costa, does not touch the end of the discal cell as it does in *G. saccoi* and *G. vanuatuensis*. In *G. eras* this line is vestigial or entirely lacking in most specimens.

The male genitalia of *G. fijiensis* (Fig. 14) differ from those of *G. vanuatuensis* (Fig. 17) in having the uncus, in lateral view, narrower, less arched, parallel-sided for nearly the whole of its length and lacks the distally enlarged apex. *Gnathothlibus vanuatuensis* also has a larger dorsal crest. When compared to *G. fijiensis*, the uncus of *G. saccoi* (Fig. 19), in lateral view, is more steeply arched, slightly wider and distally enlarged without a dorsal crest. The sacculus process is not as robust as it is in *G. eras* (Fig. 18) and *G. vanuatuensis* and the upturned distal end of the harpe is slightly more needle-like and straight-sided than in either *G. vanuatuensis* or *G. eras*. The valvae are clearly narrower between the dorsal and ventral margins than in *G. vanuatuensis* and *G. eras*. *G. eras* also has a clearly concave dorsal margin which is straight in *G. fijiensis*.

When placed in series, or side by side as individuals, all four species are readily separated by their different external morphological characters.

Gnathothlibus samoaensis n.sp.

Figs 5–9, 16

Type material. HOLOTYPE ♂, SAMOA: Approx. 10 km S-W of Apia, Upolu Is. Alt. 410 m. 13°52'53.9"S 171°49'26"W 18 Nov. 2008, R.B. Lachlan, AM K266028. PARATYPES 52♂♂, 4♀♀, all with same data as holotype but dated between 13th and 19th November, 2008. 4♂♂ and 1♀ (AM K266029–K266032, and K266033♀) in AM, remainder in RBLC.

Other material examined. 3♂♂, WESTERN SAMOA: Mulivai Beach area, central south coast of Upolu Island, 9, 12 May, 1985, R.B. Lachlan, in RBLC.

Diagnosis. Head, thorax and abdomen uniform olive-green. Forewing upperside olive green in colour with prominent darker markings. The unicolorous band enclosing the stigma is about 5 mm wide along vein CuA_1. Hindwing upperside ground colour orange; a dark, slightly variable, well-developed terminal band from apex to tornus at least 2 mm wide with most specimens exhibiting some dark scaling along inner margin from tornus. Female forewing upperside with ground colour and pattern in shades of darkish brown, lacking olive green tinge of male but with a lustrous appearance in fresh specimens, particularly on the median and marginal areas of wing.

Description. Male. (Figs 5,6,9,16). Antennae creamy-brown above, brown below; palpi olive green above, contrasting off white below; dorsal surface of head and prothorax darker olive green, remainder of thorax and abdomen uniform olive green; small dark median spot with vestigial posterolateral orange-brown on prothorax; thin lateral creamy-olive stripe from base of antenna to costa of forewing, continuing as creamy-white on the outer edges of the tegula above both wings. Thorax ventrally with creamy, light brown patch immediately posterior to palpi, remainder of narrow median band creamy-olive edged laterally with reddish-brown pilosity, dissipating as it reaches upper abdominal segments. Abdominal segments laterally (Fig. 9) each with distinct orange-brown posterior margin contrasting with olive green ground colour; abdomen with three small lateral black spots surrounded clearly by white. Fore-tibae covered in long, creamy, light olive hairs cales with very distinct dark, distal, ventral edge; proximal three segments of fore-tarsi covered in short, creamy hair scales above, edged ventrally with cream hair scales suffused with dark scales, shortest on distal segment, longest on proximal segment.

Forewing upperside as in Fig. 5. Forewing length 35.4–44.3 mm, mean 40.4 mm (n = 68). Ground colour olive green (brighter in fresh specimens) with darker markings on distal area of wing; some specimens appear browner but dark olive-green scaling is still clearly present on the forewings and body to varying degrees; small black stigma with light coloured centre at end of discal cell; small, dark, postmedian line from costa to vein M_1 becoming a line of dark dots on each vein to vein 1A+2A; irregular submarginal patch of dark scales from vein M_1 to vein CuA_1; this patch is variable; a prominent, dark, straightish oblique median line runs from costa, where it is curved distally, to inner margin; a short, irregular, subbasal band edged on each side by thin dark lines and curved gently distally, runs from costa to the dark basal

Fig. 1. *Gnathothlibus fijiensis* n.sp. holotype male, upperside.

Fig. 2. *Gnathothlibus fijiensis* n.sp. holotype male, underside.

Fig. 3. *Gnathothlibus fijiensis* n.sp. paratype female, upperside.

Fig. 4. *Gnathothlibus fijiensis* n.sp. paratype female, underside.

Fig. 5. *Gnathothlibus samoaensis* n.sp. holotype male, upperside.

Fig. 6. *Gnathothlibus samoaensis* n.sp. holotype male, underside.

Fig. 7. *Gnathothlibus samoaensis* n.sp. paratype female, upperside.

Fig. 8. *Gnathothlibus samoaensis* n.sp. paratype female, underside.

Fig. 9. *Gnathothlibus samoaensis* n.sp. holotype male, lateral view showing colouration of abdominal segments.

patch below vein 1A+2A. The unicolorous band enclosing the stigma is about 5 mm wide along vein CuA_1. Forewing underside as in Fig. 6; ground colour burnt orange basad, distally overlaid heavily with darker olive-brown scales with usually two distinct dark, irregular, parallel post median lines from costa to veins CuA_1 or CuA_2 and a single distinct, dark, irregular, submarginal line from apex to tornus; all three lines are usually well developed, particularly the submarginal line but may be reduced in some specimens.

Hindwing upperside as in Fig. 5; ground colour orange; a dark, slightly variable, well-developed terminal band from apex to tornus at least 2 mm wide, slightly thinner near apex with most specimens exhibiting some dark scaling along inner margin from tornus; inner edge of terminal band clearly spikes basally along vein 1A+2A. Hindwing underside as in Fig. 6; ground colour orange-brown, very heavily speckled with dark brown and olive scales; marginal area darker from apex to tornus; dark, mostly straight, median line, thickest at costa, curving distad from costa to vein RS and usually reaching vein CuA_2 but does not touch distal edge of cell; a much less prominent, small, parallel, dark post median line to vein M_1, well developed in many specimens, vestigial in some specimens.

Male genitalia as in Fig. 16. Uncus, in lateral view, long, slender, parallel sided for the basal half of its length, slightly but clearly arched, distal end swollen, distal margin clearly convex with rounded, slightly pointed dorsal crest; small, sharply pointed ventral tooth at distal margin; gnathos, in lateral view, thin, almost straight, dorsal surface tapering to a small, slightly upturned point at distal margin, ventral surface slightly concave; valva dorsal margin straight proximally then clearly upwardly convex, distal margin rounded, ventral margin slightly convex; sacculus well developed; harpe robust, distal end smooth surfaced and spine-like, upturned; aedeagus in lateral view, with distal end tapered to a bluntly rounded apex with backward directed dorsal fishhook-like barb, ventrally with a small, similar barb, a little proximad of dorsal barb.

Female. (Figs 7,8). Forewing length 43.6–46 mm, mean 44.7 mm (n = 4). Head, thorax and tegulae dark brown. Abdomen above dark grey-brown. Thin lateral creamy-yellow stripe from base of antenna to posterior edge of tegulae above hindwings. Thorax below reddish-brown suffused ventrally with mauve hair scales; abdomen ventrally mauve-brown, each segment with orange-brown hair scales on posterior margin with four well-developed lateral white spots with small black centres. Fore-tibiae covered in short cream hair scales with some dark scales on distal posterior edge; fore-tarsi without hair scales.

Forewing upperside as in Fig. 7; ground colour and pattern in shades of darkish brown, lacking olive green tinge of male but with a lustrous appearance in fresh specimens, particularly on the median and marginal areas of wing; small dark brown stigma with light centre at end of discal cell; a distinct lighter, lustrous brown band, enclosing the stigma, runs from costa to inner margin, marginal band from apex to tornus, with inner irregular line, of same colour. Forewing underside as in Fig. 8; ground colour reddish-brown, marginal band from apex to tornus mauve-brown and often overlaid distinctly with olive scales, a dark brown, irregular, submarginal line runs from apex to tornus; two variable dark brown parallel post median lines run from costa, often reaching vein CuA_2.

Hindwing upperside as in male but dark brown terminal band much broader, with inner margin slightly irregular and suffused with orange scales, this dark band spikes distinctly basad along vein 1A+2A. Hindwing underside as in Fig. 8; ground colour slightly more mauve than forewing and heavily speckled along costa with dark scales; slightly variable yellowish streak, mostly along proximal side of vein 1A+2A.

Etymology. The specific name *samoaensis* is derived from the Pacific Island nation of Samoa, formally Western Samoa, the only recorded locality for the species.

Distribution. At present *G. samoaensis* is only recorded from the island of Upolu, Samoa, but being a common species it would certainly be found on the nearby larger island of Savai'i, just 22 km west of Upolu.

Discussion

Although similar in overall appearance, the males of *G. samoaensis* are readily distinguished from *G. fijiensis* males by a variety of constant morphological differences. On the forewings, the prominent dark, post median oblique line that runs from the costa to the inner margin, is clearly straighter and less curved distally near the costa in *G. fijiensis*. The unicolorous median band enclosing the stigma that runs from the costa to the inner margin, is approximately 2–3 mm wider, on average, on *G. fijiensis*.

On the hindwings of *G. samoaensis* the inner edge of the dark terminal band is more irregular and less even than seen on *G. fijiensis*. The inner edge of this band clearly spikes basally along vein 1A+2A with some brown scaling basad along the inner margin past the tornus in almost all specimens examined. Neither characters appears on *G. fijiensis*.

The very distinctive mauve lateral stripe on the outer edges of the tegulae above the wings of *G. fijiensis* is creamy-white on *G. samoaensis*. Immediately behind this creamy-white lateral stripe is a small, distinctive, patch of long orange-brown hair scales. These are cream to olive-cream in *G. fijiensis*.

The underside of both wings of *G. samoaensis* are darker with generally more prominent post median and submarginal dark brown lines on the forewings than seen on *G. fijiensis*. On the underside of the thorax the ventral creamy-olive median band is shorter and narrower on *G. samoaensis* than seen on *G. fijiensis* where it is clearly longer and wider. *Gnathothlibus samoaensis* has fore-tibiae that are slightly lighter with a more distinctive dark, distal, ventral edge. The mid and hind legs are also lighter in colour than seen on *G. fijiensis*.

The male genitalia of *G. samoaensis*, Fig. 16, differ from those of *G. fijiensis*, Fig. 14, in having the uncus, in lateral view, more arched, more enlarged distally with a larger, more robust rounded dorsal crest and a clearly smaller, more pointed ventral tooth at the base of the distal margin. The distal margin is clearly concave and not angled backwards as seen in *G. fijiensis*. The sacculus process and harpe are slightly larger with a thicker, upturned spike in *G. samoaensis*. The upturned spike is finer and more needle-like in *G. fijiensis*. The valva of *G. samoaensis* differ from *G. fijiensis* primarily in having a very clear convex distal bulge on the dorsal margin. In *G. fijiensis* this dorsal margin is very slightly concave.

As in the males, the females of *G. samoaensis* differ from those of *G. fijiensis* on the forewings in having a less straight prominent, oblique, dark brown, post median line and narrower unicolorous median band enclosing the stigma. On the hindwings, the dark brown terminal band on *G. samoaensis* has a more irregular inner edge than *G. fijiensis* and also spikes clearly basally along vein 1A+2A. The additional brown scaling along the edge of the inner margin basally from the tornus is also far more evident in *G. samoaensis*. The creamy-yellow lateral stripe from the antenna to the posterior margin of the tegula above the hindwings in *G. samoaensis* is much whiter in *G. fijiensis*. Immediately behind this stripe is a small, distinct patch of long orange-brown hair scales in *G. samoaensis*; these are creamy-yellow in *G. fijiensis*. The underside of the forewings and hindwings tend to be darker in *G. samoaensis*. The fore-tibae hair scales of *G. samoaensis* are cream with some dark scales; in *G. fijiensis* the cream is usually heavily suffused with pinkish-brown scales.

Gnathothlibus samoaensis is readily distinguished from *G. eras* by the distinctive olive green colouring and more prominent markings, including the stigma, on the forewings of the male. The head, thorax, dorsal and lateral surfaces of the abdomen of the male are also olive green, these are brown in *G. eras*, as are the forewings. Even in specimens of *G. samoaensis* that show reduced overall green coloration, there is clear evidence of some degree of greenish scaling on the wings and body. Behind the thin lateral creamy-white stripe above the wings is a small distinctive patch of orange-brown hair scales on each side of the abdomen of *G. samoaensis*, these patches are creamy in *G. eras*. The dark brown terminal band on the hindwings of the males tends to be slightly wider in most specimens of *G. samoaensis* than seen on *G. eras* where it is often very narrow. Some brown scaling is also evident along the inner margin basally from the tornus in *G. samoaensis*. The dark brown terminal band stops at vein 1A+2A in *G. eras*.

The long hair scales on the fore-tibae and fore-tarsi are slightly shorter on *G. samoaensis* than seen on *G. eras*. On the underside of the males of *G. samoaensis* the two dark, irregular, parallel, post median lines and the irregular submarginal line from apex to tornus on the forewings and the median and less obvious post median line on the hindwings are usually very evident to varying degrees. In *G. eras* usually only the dark submarginal line on the forewing is visible and often only to vein M_3. The others are almost always vestigial or absent.

The male genitalia of *G. samoaensis* (Fig. 16) differ from those of *G. eras* (Fig. 18) in having the uncus, in lateral view, longer, less distally enlarged, with a more rounded dorsal crest, a more concave apical margin and a smaller, pointed ventral tooth; in *G. eras* the dorsal crest is higher and more pointed and the apical margin is clearly straighter. Gnathos, in lateral view, slightly shorter and lacks the small upturned distal point seen in *G. eras*; in dorsal view, *G. samoaensis* has straighter sides and a blunt point, in *G. eras* the sides are clearly convex tapering to a sharper point.

The specimens of *G. samoaensis* examined that showed less green appeared to be generally older which suggests that the green coloration may fade, to some degree, with age and exposure to light.

Given that large numbers of only *G. samoaensis* were collected and sighted in November 2008 and other specimens in May 1985, it appears that *G. eras* does not occur on the Samoan islands despite being recorded from as far east as Tahiti.

It should be noted that the closest populations of *G. eras* and *G. fijiensis* are to be found on the Fijian islands, some 800 km southwest of Samoa. When placed in series, or side by side as individual specimens, all three species can be readily separated by their external morphological characters alone.

Fig. 10. *Theretra tabubilensis* n.sp. holotype male, upperside.

Fig. 11. *Theretra tabubilensis* n.sp. paratype female, upperside.

Fig. 12. *Theretra indistincta papuensis* lectotype male, upperside.

Fig. 13. *Theretra indistincta papuensis* lectotype male, underside.

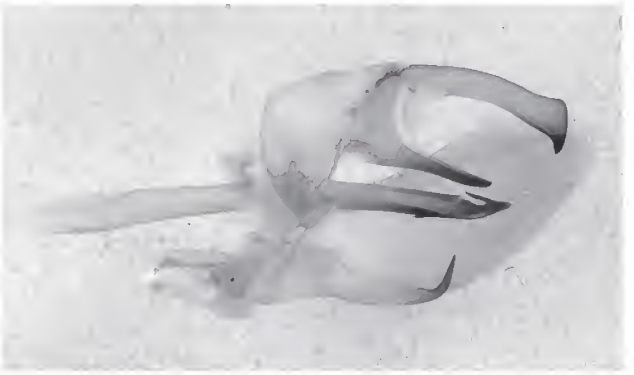

Fig. 14. *Gnathothlibus fijiensis* n.sp.

Fig. 15. *Gnathothlibus australiensis*.

Fig. 16. *Gnathothlibus samoaensis* n.sp.

Fig. 17. *Gnathothlibus vanuatuensis*.

Fig. 18. *Gnathothlibus eras*.

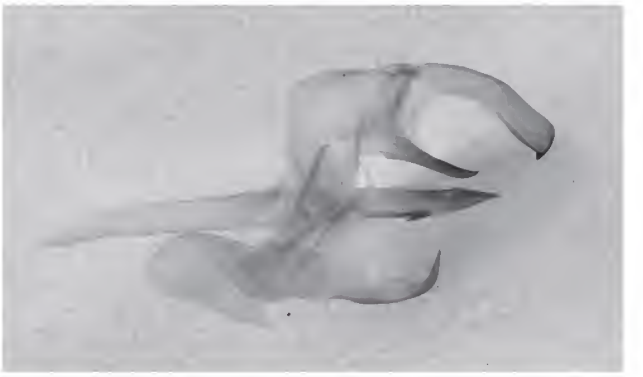

Fig. 19. *Gnathothlibus saccoi*.

Fig. 20. *Theretra tabubilensis* n.sp.

Fig. 21. *Theretra indistincta papuensis*.

Genus *Theretra* Hübner, [1819]

Type species: *Choerocampa indistincta* Butler, 1877.

Lectotype designation for *Theretra indistincta papuensis* Joicey & Talbot

Figs 12, 13

Joicey and Talbot (1921) described *papuensis* as a subspecies of *Theretra clotho*. Later, Jordan (1926) synonymized *Theretra clotho papuensis* placing it as a subspecies of *Theretra indistincta*.

Theretra clotho papuensis was described from a series of six males and five females from "Wandammen Mountains, Dutch New Guinea, 3000–4000 ft., November, 1914, A., C. & F. Pratt, 6♂♂, 4♀♀; 6000 ft., 1♀". Of these, five males and three females from 3000–4000 feet, and the female from 6000 feet, have been located in the BMNH. The remaining pair has not been found and it is likely that they were exchanged by Joicey in the 1920s. Indeed, only four of the males and two of the females from 3000–4000 feet arrived at the BMNH by being presented by J.J. Joicey in 1931 (BMNH accession number 1931-444); the remaining pair and the female from 6000 feet arrived later in 1941 as part of the Levick bequest (BMNH accession number 1941-83).

Of the syntypes of *Theretra clotho papuensis* in the BMNH, two males and two females agree with the concept of *Theretra indistincta papuensis* as I here restrict it; the other three males and two females (including that from 6000 feet) are *Theretra tabubilensis* n.sp. The syntype series is thus mixed, and so to stabilize the nomenclature, I hereby designate as lectotype the male in the BMNH, which agrees with the concept of *Theretra indistincta papuensis* (Figs 12,13), with the following labels: "LECTO-/TYPE" (small, circular, printed, purple-bordered label); "Wandammen Mts./ 3–4000 ft. D. N. Guinea./ Nov. 1914. A. C & F. Pratt" (rectangular [printed label); "Theretra/ clotho/ papuensis J. & T./TYPE. H. T." (rectangular handwritten label); "Presented by/ J.J.M Joicey, Esq./ Brit. Mus. 1931-444." (rectangular, printed label).

Theretra tabubilensis n.sp.

Figs 10, 11, 20

Type material. HOLOTYPE ♂, PAPUA NEW GUINEA. Tabubil, Western Province, 5°15'S 141°13'E. Alt. 650 m. 22 Sept. 1992, R.B. Lachlan AM K266034. PARATYPES 3♂♂ same data as holotype except dated 28 Oct. 1992, 19 Nov. 1992, 29 Nov. 1992; 1♂ SE slopes of Mt Akrik (Ian), 15 km NW of Tabubil, W.P., 5°10'S 141°09'E, Alt. 1625 m, 14 Apr. 1994, R.B. Lachlan; 1♂ Kiunga, north Fly River, W.P. 6°08'S 141°17'E, 15 Nov. 1992, R.B. Lachlan; 1♂ 30 km E of Tari, S. H. P. 5°58'S 143°07'E, Alt. 2300 m, 3 Oct. 1992, R.B. Lachlan; 11♀♀ same data as holotype except dated 15 Mar. 1991, 5 Nov. 1991, 27 Mar. 1992, 11 Oct. 1992, 28 Oct. 1992, 8 Nov. 1992, 22 Mar. 1993, 4 Oct. 1993, 12 Nov. 1993, 5 Apr. 1994, 10 Jan. 2000; 1♀ Matkomrae (Matkomnai) Catholic Mission, 50 km NNW of Kiunga, W.P. 5°49'S 140°09'E, Alt. 60 m, 6 Nov. 1993, R.B. Lachlan, all specimens in RBLC; 2♀♀ Kiunga, north Fly River, W.P. 6°08'S 141°17'E, 15 Nov. 1992, R.B. Lachlan AM K266035 and RBLC.

Other material examined. 2♂♂, 3♀♀, same data as holotype except dated 29 Mar. 1992 (2), 3 Nov. 1992, 11 Nov. 1993 (2); 1♂ Se slopes of Mt Akrik (Ian), 15 km NW of Tabubil, W.P. 5°10'S 141°09'E, Alt. 1625 m, 26 Sept. 1993, R.B. Lachlan, all in BMNH.

Other material. 1♀ "B.C. New Guinea, Mount Kebea, 6,000 ft., March-April 1903, A.E. Pratt", 1♂ "B.C. New Guinea, Mount Kebea, 3,600 ft., July 1903, A.E. Pratt", 1♂ "B. New Guinea, Mafalu, 6,000 ft., September 1903, A.E. Pratt", 1♀ "N. Dutch New Guinea, Waigeu, Camp Nok, 2,500 ft., v.1938, L.E. Cheesman" and 1♀ "Dutch New Guinea, Central Arfak Mts., Ninay Valley, 3500 ft., Nov '08 to Jan. '09", all in BMNH.

Diagnosis. Forewing with single, almost straight, olive-brown oblique line from apex to near centre of inner margin. Small, diffuse, dark patch distad of stigma near costa, not reaching oblique line. Anal area of hindwing light creamy-brown, remainder of wing dark brown with lighter creamy-brown patch at distal end of vein CuA_2. Aedeagus, viewed laterally, with convex distal margin and a line of dense, short spines angled backwards from the dorsal surface of distal margin to lateral surface. Female almost identical to male, often slightly darker.

Description. Male. Fig. 10. Antennae creamy-pink above, ventrally light brown; palpi olive-brown above, suffused with cream below; upper surface of head and thorax uniform olive-brown, slightly lighter on dorsal surface of abdomen with lightly scattered suffusion of black scales; small dark spot on prothorax; thin lateral creamy-olive brown stripe above palpi to base of tegulae above hindwings. Thorax, laterally, with dense darker olive-brown pilosity from head to base of forewings, small patch of orange-brown pilosity near base of forewings; creamy-brown along length of abdomen with diffuse, dark, lateral patch extending distally from near base of hindwing about 10 mm along abdomen; ventral abdominal segments light creamy-brown suffused with black scales. Fore-tibae creamy-olive brown, fore-tarsi without long hair scales.

Forewing upperside as in Fig. 10. Forewing length 32.5–38.7 mm, mean 35.9 mm (n = 10). Ground colour in shades of lighter and darker olive-brown, slightly variable; very small dark olive-brown stigma at distal end of discal cell; single prominent, almost straight, olive-brown line from apex, where it curves slightly distally, to just distad of halfway point of inner margin; this line unbroken at apex in almost all specimens examined; costa dark olive-brown, proximal side of oblique line slightly lighter than distal side of oblique line; small, diffuse, darkish patch just distad of stigma; proximal half of forewing very lightly speckled with dark scales, distal half more heavily speckled; single, faint, irregular, darkish subbasal line from costa to vein 1A+2A; small, rounded darkish patch at base on posterior half of forewings, continuing as flattened light then darkish wedge-like marking along inner margin, its point almost touching the dark oblique line. Forewing underside with dark tan region basally extending past discal cell, medium tan on remainder of proximal half of wing, light tan on submarginal area from apex to tornus, whole underside, except dark basal region,

clearly speckled with black scales.

Hindwing upperside as in Fig. 10. Ground colour darkish brown, small, pale, creamy-brown patch between veins CuA_2 and 1A+2A, then darkish brown streak to tornus; thin, pale, creamy-brown patch from tornus along inner margin to base. Hindwing underside with basal region pale tan, distal region darker as in distal region of forewing but with faint pinkish tinge, speckled, as in forewing, with a row of oblique, post median darkish dots from costa, where they curve distally, down to vein CuA_2.

Male genitalia. Fig. 20. Uncal lobe, in lateral view, gently arched, slender centrally with slightly enlarged distal region, ventral surface of distal margin with blunt, downward point; gnathos short, evenly curved upwards, dorsal surface slightly serrated at distal end; aedeagus, in lateral view, long, slender, parallel sided, distally enlarged with a line of dense, short spines angled from the dorsal surface to the lateral surface; distal margin with small blunt point at tip of dorsal surface, then angled backwards with small inward curve then clear convex bulge to ventral surface; harpe small, volcano-like with tiny serrations on concave dorsal surface.

Female. Fig. 11. Forewing length 34.2–40.7 mm, mean 38.2 mm (n = 17). Overall appearance, upperside and underside, is identical to male but ground colour usually slightly darker.

Etymology. The specific name, *tabubilensis*, is derived from the mining town of Tabubil in the Western Province of Papua New Guinea, where most specimens were collected.

Distribution. At present most specimens have been recorded from the Tabubil area in the central far west of PNG near the border with Indonesia, 3 specimens have been recorded approximately 90 km to the south at Kiunga on the Fly River and 1 specimen from approximately 30 km east of Tari in the Southern Highlands Province, some 200 km ESE of Tabubil. Other specimens held in The Natural History Museum, London, include specimens from Waigeu Island, just off the northwest coast of New Guinea and the Arfak Mountains in the far northwest of Indonesian New Guinea. It appears to be primarily a mountain species.

Discussion

Theretra tabubilensis most closely resembles the sympatric species *Theretra indistincta papuensis*. Over a period of several years both species were regularly collected together with no intergrade specimens encountered during the survey period. *Theretra tabubilensis* was found to be less common. There are a number of constant external morphological differences that readily separate the two species.

Theretra tabubilensis is a clearly smaller species than *T. i. papuensis* particularly in regard to the females. This is very noticeable when both species are placed in series together. *Theretra i. papuensis* is a quite unicolorous grey species whereas *T. tabubilensis* is a lighter species with forewings that have differing colour tones on each side of the dark oblique line. A distinct difference is the dark oblique line on the forewing. On *T. tabubilensis* it is a distinct, almost always unbroken line as seen on *T. clotho celata* but in *T. i. papuensis* it is much fainter and usually both broken at the radial vein immediately above vein M_1 and faint near the apex. Also, this oblique line often curves slightly towards the costa in *T. i. papuensis* but in *T. tabubilensis* it often curves slightly towards the termen. In *T. tabubilensis* the small diffuse dark marking on the forewing, distad of the stigma near the costa, does not reach the dark oblique line. In *T. i. papuensis* this diffuse dark marking is much larger and wider and reaches the tornal area of the forewing. These markings are the same on both sexes in each species.

In *T. tabubilensis* males and females, the distal point of the narrow, dark, basal streak along the inner margin of the forewing, touches, or nearly touches, the dark oblique line. In *T. i. papuensis* this thin dark basal streak does not reach the oblique line and the distal point is usually several millimetres proximad of the oblique line. This applies to both sexes. The dark basal spot on the forewing of both sexes of *T. i. papuensis* is both paler and reduced in size on both sexes of *T. tabubilensis*. On the hindwing of both sexes of *T. tabubilensis* the light creamy-brown area from the base to the tornus between the inner margin and vein 1A+2A is the same as seen on *T. clotho celata*, although not as yellow-brown. In *T. i. papuensis* this area on both sexes is clearly suffused, to varying degrees, with darker scales giving a shaded appearance.

The abdomen of *T. tabubilensis* has a longer diffuse darkish patch extending laterally halfway down the abdominal segments from near the base of the hindwings. In *T. i. papuensis* this darkish patch is reduced to a spot and does not extend laterally along the abdominal segments. On the underside of *T. tabubilensis* there is small, isolated lateral patch of orange-brown pilosity near the base of the forewings. On *T. i. papuensis* this patch is not as distinct and when visible, is a lighter salmon-pink which also usually occurs in small lateral patches along the sides of the abdomen. There is no such lateral colouring on the abdomen of *T. tabubilensis*.

The male genitalia is very similar to that of *T. clotho celata*, including the convex distal margin of the aedeagus. In *T. i. papuensis* (Fig. 21) this distal margin on the aedeagus is slightly concave. In *T. tabubilensis* the gnathos, in lateral view, appears slightly longer and thinner than seen in *T. i. papuensis* and *T. clotho celata* where it is shorter and slightly thicker.

Clearly all three species are closely related when their genitalia are examined, but there are notable, constant external morphological differences separating the three species.

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A New Species of the Genus *Mecyclothorax* Sharp from New South Wales (Insecta: Coleoptera, Carabidae: Psydrinae)

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ABSTRACT. *Mecyclothorax moorei* n.sp. (Insecta: Coleoptera: Carabidae: Psydrinae) is described from northeastern New South Wales, Australia. The species is closely related to *Mecyclothorax punctatus* (Sloane) which is distributed from inland southern New South Wales through Victoria into southwestern Western Australia. The new species and *M. punctatus* are distinguished from all other Australian species of *Mecyclothorax* by small size, compact body shape, and remarkably coarse punctation of the pronotum and elytra.

BAEHR, MARTIN, 2009. A new species of the genus *Mecyclothorax* Sharp from New South Wales (Insecta: Coleoptera, Carabidae: Psydrinae). *Records of the Australian Museum* 61(1): 89–92.

Psydrinae (or Psydrini) is a diverse subfamily (or tribe) of carabid beetles, in terms of general morphology and habits. These beetles live in leaf litter on the ground in closed forests, and on or under bark of a variety of trees in forest, woodland, and even fairly dry areas (Baehr, 2003, 2005, 2007). With respect to lineages and to morphology worldwide, the group is most diverse in Australia (Moore, 1963; Moore *et al.*, 1987; Baehr, 1999) and many subgroups have representatives in cool or even cold temperate habitats, not only in Australia, but also in New Zealand, southern South America and on a number of subantarctic islands. Some groups, however, transgressed the southern cool temperate region and moved in to tropical (mostly montane) regions, for example, in northern Queensland and New Guinea, as well as certain Pacific island groups, where they have undergone remarkable radiation (Baehr, 1995, 1999, 2003, 2005, 2007; Larochelle & Larivière, 2007; Liebherr, 2006, 2008; Moore, 1984; Moore *et al.*, 1987; Perrault, 1978, 1992). A few species even occur in Africa and the Holarctic region.

One of the most prolific genera of Psydrinae, in terms of numbers of existing species, is the genus *Mecyclothorax* Sharp, 1903 which is widely distributed in the Australian-Pacific area including New Guinea, New Zealand, Tahiti, and Hawaii, with one species even occurring on Mt. Kinabalu in northern Borneo (Baehr & Lorenz, 1999). In Australia, (including Norfolk and Lord Howe Islands and Tasmania) 23 taxa of *Mecyclothorax* have so far been recorded; they range from Atherton and Windsor Tablelands along the east coast through Queensland and New South Wales, through Victoria, Tasmania, and southern South Australia to southern Western Australia. Moore (1984) and Baehr (2003) published partial taxonomic treatments, but a number of very similar species are still in need of revision.

During a recent visit to the Australian Museum, Sydney, and while checking the collection for additional material for forthcoming revisions of Australian carabid beetles, I found three specimens of an unusual, small, *Mecyclothorax* beetle. A decade ago the specimens had already been denoted as a new species by Barry Moore. Comparison with the only other similar Australian species, *Mecyclothorax punctatus* (Sloane, 1895), confirmed that the specimens indeed belong to a separate and closely related species which is described below.

Methods

Measurements were taken using a stereo microscope with an ocular micrometer. Body length was measured from apex of labrum to apex of elytra. Body lengths, therefore, may slightly differ from those specified by other authors. Length of pronotum was measured from mid of apex to the most advanced part of base. Length of elytra was measured from the most advanced part of humerus to the very apex.

In the taxonomic survey standard methods are used. The male genitalia were removed from a specimen after being relaxed overnight in a moisturizing jar, then briefly cleared in hot KOH. The habitus photograph was manipulated using SPOT Advanced for Windows 3.5 and Corel Photo Paint 11.

The male holotype and one female paratype of the new species are located in the Australian Museum, Sydney (AMS), one female paratype is located in the working collection of the author at Zoologische Staatssammlung, München (CBM).

Taxonomy

Mecyclothorax Sharp, 1903

Mecyclothorax Sharp, 1903, *Fauna Hawaiiensis* 3: 243, 1901–1910. Type species: *Cyclothorax montivagus* Blackburn, 1878, designated by Andrewes, 1939: 135. Geographic distribution: Australia, New Zealand, Pacific Islands.

Mecyclothorax moorei n.sp

Figs 1–3

Type material. HOLOTYPE ♂, site 32AR NSW Banda Rd about 4.5 km E of Hastings Forest Hwy 31°09'S 152°25'E Mount Boss State Forest 17 1100m (NPWS Survey) 4 Feb–9 Apr 1993 M. Gray, G. Cassis (AMS K241125). PARATYPES, 1 ♀, same data (CBM); 1 ♀, site 20BG NSW: Main Ck, track off Mt Tindal Td 29°43'S 152°38'E Ramornie SF 92 110m (NWPS Survey) 4 Feb–9 Apr 1993 M. Gray, G. Cassis (AMS K241131).

Fig. 1. *Mecyclothorax moorei* n.sp., female paratype, habitus. Body length: 3.25 mm.

Diagnosis. Small, compact, dorsally convex species, characterized by exceptionally coarse punctation of the upper surface of the pronotum and the elytral striae. Distinguished from the only similar species, *Mecyclothorax punctatus* (Sloane), by shorter and more oviform elytra, much more abbreviated elytra striae, and far less dense punctation of the pronotum.

Description. *Measurements.* Length: 3.0–3.25 mm; width: 1.2–1.4 mm; ratios: width/length of pronotum: 1.26; width base/apex of pronotum: 1.13–1.16; width pronotum/head: 1.41–1.44; length/width of elytra: 1.27–1.33; width elytra/pronotum: 1.32–1.40.

Colour. Rusty red, centre of head, pronotum, and disk of elytra darker, piceous to almost blackish, but dark colouration of elytra very ill delimited. Suture, base, and margins of elytra reddish, antennae reddish, mouth parts and legs dirty yellow. Lower surface of head, prothorax, and middle of abdomen piceous, rest reddish.

Head. Considerably narrower than pronotum. Eyes laterally projected, orbits short, c. ⅛ of length of eye, forming a distinct angle with the lateral part of the head. Eyes separated from frons by a narrow furrow. Frontal furrows very deep, irregularly sinuate, running from clypeal seta, then suddenly turned out towards the eye, ended at anterior supraorbital seta. Centre of frons and lateral parts outside of frontal furrows convex. Clypeal suture deep, clypeus bisetose, punctures large and deep. Labrum anteriorly very slightly concave, six-setose. Mandibles of moderate size, at apex suddenly incurved. Seta in outer scrobe elongate. Mentum with wide, obtuse, triangular tooth. Two mental setae and four gular setae present, all setae very elongate. Glossa truncate at apex, rather narrow, bisetose, paraglossae membranous, far surpassing glossa. Lacinia elongate, sparsely spinose at inner margin. Terminal palpomeres of

both palpi asetose. Antenna short, antennomeres 7–10 c. 1 ⅓ × as long as wide. Posterior supraorbital seta situated slightly in front of posterior margin of eye. Upper surface of head without any microreticulation, impunctate apart from a few very coarse punctures on lateral parts of frons near the eyes. Surface very glossy.

Pronotum. Wide, laterally and dorsally convex. Apex straight or even slightly convex, apical angles not produced. Lateral margins in apical half markedly convex, in basal half straight and oblique, just in front of basal angles shortly and weakly sinuate. Basal angles angulate and slightly produced. Base in middle straight, laterally slightly excised. Both, apex and base not margined, marginal sulcus narrow throughout, not widened towards base. Median line fine and inconspicuous, not attaining apex nor base. Basal grooves deep, short, linear. Anterior transversal sulcus barely indicated, basal transverse sulcus fairly deep. Both marginal setae present, the anterior one situated at the widest diameter at or slightly in front of middle, the posterior one at basal angle. Disk with sparse, very coarse, and somewhat irregularly spaced punctures, distance between punctures at least as large, and mostly much larger than diameter of punctures. Surface without any microreticulation, absolutely smooth, very glossy.

Elytra. Very short and wide, dorsally very convex, remarkably oviform. Humeri wide, very gently angulate, lateral margin convex throughout. Base completely bordered. Scutellar stria indicated only by one or two large punctures, situated in first interval, scutellar pore and seta situated at or slightly laterad of origin of first stria. First stria slightly impressed and marked by a row of coarse punctures, stria ends at apical third or fourth of elytra. Other striae very vaguely indicated as rows of scattered, rather coarse punctures, but almost the whole surface without distinct striae. Intervals apart from first absolutely depressed. Dorsal setiferous punctures situated at position of third stria, rather inconspicuous, the anterior one situated in or slightly behind basal third, the posterior one situated at apical third. Setae elongate. Series of marginal setae consisting of 7 anterior and 5–6 posterior setae that are widely separated in middle, punctures coarse, setae, if unbroken, very elongate. At the position where the third and fifth intervals would end, either with a short seta. Intervals without any microreticulation and punctures, absolutely smooth, very glossy. Posterior wings very short.

Lower surface. Lateral parts of prothorax and mesothorax, and prosternum with dense and very coarse punctures, the diameter of which is larger than the distance between the punctures. Metepisternum short, quadrate. Surface of abdomen without any microreticulation and punctures, glossy. Terminal sternum in both sexes quadrisetose.

Legs. Moderately elongate. Four basal tarsomeres of male protarsus slightly widened, first to third tarsomeres asymmetrically squamose on lower surface. Mesotibia and metatibia with remarkably distinct microreticulation on the upper surface.

Male genitalia (Fig. 2). Genital ring moderately elongate, asymmetrically triangular, apex moderately wide, fairly elongate. Aedeagus slightly turned to the left side (in beetle), rather short and compact (in genus), lower surface evenly concave, in front of apex slightly more curved down. Apex short and wide, probably obtuse at tip, but the very tip in the single male destroyed. Ostium rather short. Internal sac rather complexly folded, with a sclerotized spine-like flagellum and several partly sclerotized plates within. Parameres dissimilar, left comparatively stout, probably with elongate, tapering, spine-like apex, but apex broken in the male. Right paramere narrow and elongate, with evenly tapering apex, with 2 short apical setae, and about six rather elongate setae along lower margin.

Female genitalia (Fig. 3). Gonocoxite 1 without any ensiform setae at ventro-apical margin. Gonocoxite 2 rather short, with short apex and two large dentiform ventro-lateral ensiform setae of about similar size below middle of lateral margin. Near apex with a large, oblong pit but apparently with only a single nematiform seta originating from that pit. In middle of dorso-median surface with a large, dentiform, dorso-median ensiform seta. Lateral plate with a densely setose area at median apical margin.

Variation. Very little variation noted.

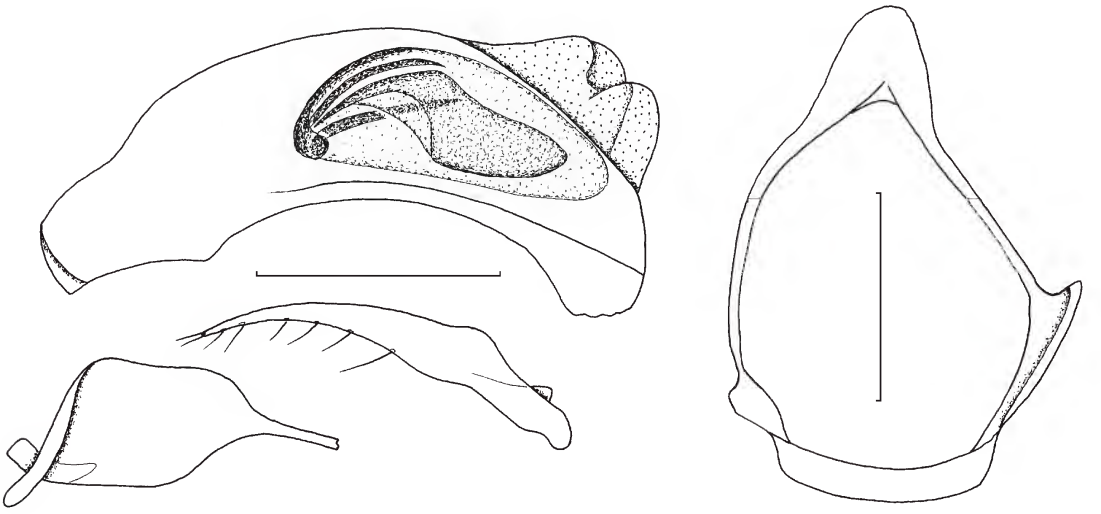

Fig. 2. *Mecyclothorax moorei* n.sp., male aedeagus, parameres and genital ring. Scales: 0.25 mm.

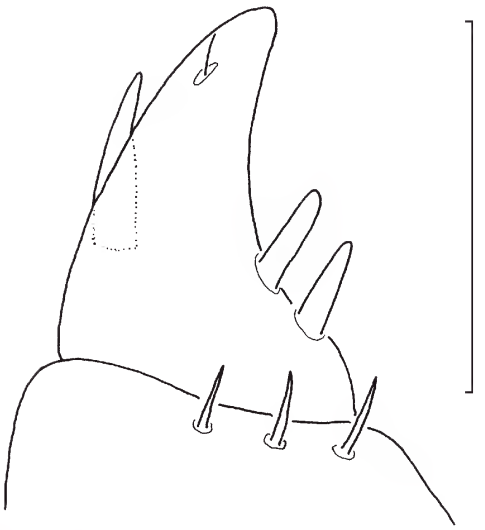

Fig. 3. *Mecyclothorax moorei* n.sp., female gonocoxites 1 and 2. Scale: 0.1 mm.

Distribution. Recorded only from a restricted area in north-eastern New South Wales.

Etymology. The specific name is a patronym in honour to Dr Barry Moore, famous senior specialist of Australian carabid beetles, who already had identified the species as a new one.

Collecting circumstances. Unknown.

Remarks

This small but distinctive species is quite different in external features from most other Australian species of the genus *Mecyclothorax*. It is similar to, and most probably quite closely related to, *M. punctatus* (Sloane). The latter has comparable compact and convex body shape and a similar, very coarse punctation of pronotum and elytral striae. The main differences are (*a*) in the shape of the elytra, they are shorter and more oviform in *M. moorei*, (*b*) the much less-dense punctation of the pronotum in *M. moorei*, and (*c*) the much more abbreviated elytra striae in *M. moorei*.

Among the Australian species of *Mecyclothorax* both *moorei* and *punctatus* form a distinct subgroup which, on the basis of external morphology, is rather different from the "normal-shaped" species of the *ambiguus-punctipennis*-lineage of the genus. With respect to body shape and small size, both species seem to be more closely related to the small species which occur in the rainforests of northern Queensland (*M. storeyi* Moore, 1984; *M. lewisensis* Moore, 1984; *M. impressipennis* Baehr, 2003; and *M. inflatus* Baehr, 2003) than to the common species in the surrounding areas, e.g., *M. punctipennis* (Macleay, 1871) and its allies.

Nothing is known about the habits and life history of the new species, apart from that it probably lives in closed forest at various altitudes, where it may occur on the ground in leaf litter.

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